The reproductive biology of Cretaceous oviraptorid dinosaurs and its implication for the origin of bird reproduction

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Tzu-Ruei YANG

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Erstgutachter und Betreuer: Prof. Dr. P. Martin Sander (FK Geowissenschaften, kooptiert in FK Biologie, Univerität Bonn)
Zweitegutachter: Prof. Dr. Eva M. Griebeler (FB Biologie, Universität Mainz)
Fachnahes Mitglied: Prof. Dr. Gerhard von der Emde (FK Biologie, Universität Bonn)
Fachfremdes Mitglied: PD Dr. Marianne Engeser (FK Chemie, Universität Bonn)

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Tzu-Ruei Yang

Forsake her not, and she shall preserve you: love her, and she shall keep you.

Proverbs 4:6, The Bible

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Summary

This dissertation aims to pioneer an integrative approach that includes all lines of evidence to comprehensively and in detail reconstruct the biology of an extinct animal. Specifically, the dissertation consists of several contributions to understanding the reproductive biology of oviraptorid dinosaurs. Oviraptorid dinosaurs are a distinctive group of feathered maniraptoran dinosaurs from the Late Cretaceous and are characterized by their toothless, parrot-like beaks. They constitute Oviraptorosauria together with Caenagnathidae. Oviraptorid dinosaurs left a superb record of skeletal fossils, clutches, and eggs that inform on their reproductive biology. For instance, an oviraptorosaurian pelvis with a pair of shelled eggs inside elucidated their intermediate stage of ovulation and oviduct function between crocodiles and birds. The endothermy inferred from bone histology and discoveries of feathered dinosaurs in the last decades demonstrated that dinosaurs were closely related to modern birds. The association of an oviraptorid adult "sitting" on a clutch is represented by several Mongolian and Chinese fossils and was interpreted as brooding behavior, a parental care mode only present in modern birds. Despite controversies over this interpretation, these amazing fossils led to the current view that the biology of these near-bird dinosaurs can be inferred from that of modern birds.

However, evidence from chemical, taphonomic, and ecological approaches presented in this dissertation reveals a unique reproductive biology in oviraptorid dinosaurs. Raman spectrometry, elemental mapping, chemometric analysis, and mass spectrometry indicate the preservation of cuticle on eggshell and tetrapyrrolic pigments in eggshell, suggested that the oviraptorid egg was cuticle-coated and its shell was blue-greenish in color. In addition to the colored eggshell, heterogeneous distribution of porosity over the egg indicates a semi-buried clutch. The investigation of several well-preserved oviraptorid clutches reveals that he oviraptorid clutch consists of three to four rings of paired eggs, the blunt end of which points to the center devoid of eggs in an inclining angle of more than 40 degrees. In ovo oviraptorid embryos at different developmental stages from the same clutch suggested hatching asynchrony, which was possibly a result of communal nesting and polygamy. All of these lines of evidence demonstrate a unique reproductive mode in oviraptorid dinosaurs that differs from modern birds in egg structure, clutch architecture and nesting mode, and from less derived dinosaurs and crocodiles in hatching mode and parental investment. Such a unique reproductive mode lacking any modern analogs is contrary to the current view that the nesting biology of these near-bird dinosaurs is analogous to that of modern birds since they are closely related.

Chapter 1 Introduction

PUBLICATION	ABSTRACT

no publication planned

Dinosaur eggs, clutches, and nests have been discovered around the world, especially in China and Mongolia. Dr. Henry Fairfield Osborn described a specimen of *Oviraptor philoceratops* clutch-adult association from Mongolia and proposed that this *Oviraptor* individual was preying on a *Protoceratops* clutch (AMNH 6517; Osborn, 1924). This genus name "Oviraptor" was later used to denote the clade Oviraptoridae, which comprises the higher clade Oviraptorosauria with the clade Caenagnathidae. However, due to the at that time insufficient understanding of which type of egg was produced by which biological species, the speculation of *Oviraptor* being an "egg thief" had long been in debate. Eventually, a pioneer scientist, Dr. Zikui Zhao from the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing, China, developed a modern parataxonomic system (Zhao, 1975). His work provided paleontologists with a common scientific language facilitating communication and allowing for hierarchical organization of egg specimens based on identifiable characters of eggshells. In 1994, following the establishment of the modern parataxonomic system, an embryo-bearing elongatoolithid egg was discovered in Ukhaa Tolgod, Mongolia, and assigned to an oviraptorid dinosaur (Theropoda: Oviraptorosauria, sometimes termed as oviraptors) based on several synapomorphies. The oviraptorid embryo-bearing egg falsified Osborn's 1924 hypothesis, demonstrating that the elongatoolithid eggs described by Osborn had been actually laid by oviraptorids rather than *Protoceratops*. In the following year, Norell et al. (1995) reported a *Citipati* clutch-adult association from Ukhaa Tolgod, Mongolia, hypothesizing that the brooding behavior—a typical

extant avian trait—had already appeared in dinosaurs. In combination with the discoveries of feathered dinosaurs from China and Canada in the last decade (Ji et al., 1998; Zelenitsky et al., 2012), brooding dinosaurs have been gradually accepted by most dinosaur paleontologists. However, the brooding hypothesis was questioned by several poultry scientists and still remains controversial. These arguments also raised a number of additional questions that are worthy of being further investigated from different perspectives and with various cutting-edge methods. The past 20 years have led to a rapid increase of knowledge on dinosaur reproductive biology thanks to a number of striking fossil discoveries, including clutch-adult associations, two gravid oviraptorosaurs, and numerous embryo-bearing eggs. These discoveries still yield great potential for extensive studies on the reproductive biology of dinosaurs. Moreover, a recent article documented these discoveries and provided a review of the evolution of reproductive biology from basal theropods to modern birds (Varricchio & Jackson, 2016). From the perspective of reproductive biology, the authors consider that the oviraptors are an intermediate group, representing a part of the continuum of the evolution toward modern birds. However, more and more evidence arising from the fossil record indicates that oviraptors exhibited a peculiar reproductive biology not analogous to that of modern birds. More reevaluation and explicit interpretations are thus necessary. This dissertation aims to elucidate dinosaur reproductive biology, especially that of oviraptorid dinosaurs. Using background information from ornithology, poultry science, and ecology and combining this with chemical analytical methods, the thesis attempts to reach a comprehensive understanding of the evolution of reproductive biology in derived theropods.

1-1 Previous Studies I: Research on Dinosaur Eggs

The mineralized eggshell is an evolutionary novelty that enables vertebrates to reproduce on land. Various features adaptations of the eggshell are adaptations to different environments and nesting strategies. All dinosaurian eggshells are composed of two to three calcareous fiber layers that show different crystallite patterns (parallel, random felt-work, or widely spaced). Pores in dinosaurian eggshells are in charge of adjusting the humidity and oxygen concentration. Already in 1923 van Straelen & Denaeyer (1923) recognized that the pores might allow inferences to be made on the microclimate of dinosaur nests. Since then many paleontologists suggested that the nesting mode of dinosaurs can be deduced by estimating the porosity and water vapor conductance of eggshells. Focusing on oviraptors, van Straelen (1925) suggested that the Mongolian oviraptorid dinosaur eggs may have been laid in an arid climate because of the low porosity of the shell. Later, both Mou (1992) and Deeming (2006) indicated that the oviraptorid eggs had relatively higher water vapor conductance, inconsistent with an arid nesting environment. A problem with the water vapor conductance estimation is that the measurements of the porosity was limited to a single piece of eggshell. Varricchio et al. (2013) measured the porosity over a *Troodon* egg and noticed that the porosity is heterogeniously distributed over the egg which could also apply to the eggs of the closely related oviraptor. Because of all of these competing theories, the porosity of oviraptorid eggs and their interpreted nesting environments are worthy of being re-investigated.

In addition to the porosity, paleontologists have long been interested in the microstructure and composition of dinosaur eggs. Unfortunately, apart from the calcareous eggshell, most soft-tissue or proteinaceous structures, such as the cuticle, the *membrana testacea*, and pigments, were considered unlikely to be preserved during fossilization. Surprisingly, recent studies revealed a great extent of soft-tissue preservation in fossils using cutting-edge chemical methods (Schweitzer et al., 2005a; Schweitzer, Wittmeyer & Horner, 2005; Schweitzer et al., 2005b; Schweitzer et al., 2007; Schweitzer et al., 2016). These new chemical techniques will help paleontologists further understand the structure of dinosaur eggshells.

Besides, the inner structure of a dinosaur egg is also unlikely preserved. However, based on indirect evidence inferred from fossil record, it was suggested that oviraptorosaurian eggs are weakly asymmetrical, implying the development of an proto-air cell in the blunt end (Grellet-Tinner et al., 2006; Varricchio & Jackson, 2016). They also demonstrated that the chalazae (a membranous strip that stabilizes egg yolk) evolved in response to eggs incubated in open nests.

1-2 Previous Studies II: Reproductive Biology of Dinosaurs

Despite numerous discoveries of dinosaur eggs around the world, most studies restricted themselves to descriptive and comparative work, without further exploration of the ecological and behavioral aspects. For instance, numerous previous reconstructions of oviraptorid clutches failed to lead to a full understanding because the detailed pattern of oviraptorid clutches had never been investigated (Norell et al., 1995; Dong & Currie, 1996; Deeming, 2002a; Fanti, Currie & Badamgarav, 2012; Varricchio & Jackson, 2016). Although the pairedness in oviraptorid clutches has been frequently observed, Varricchio & Jackson (2016) considered that the pairedness in oviraptorid clutches has never been rigorously statistically tested. The pairedness in oviraptorid clutches is hence representative of a clutch without any postlaying manipulation. In addition to the pairedness, the highly organized arrangement in oviraptorid clutches has been documented (Zelenitsky, 2006) but not well investigated.

Norell et al. (1995) proposed that the bird-like brooding behavior already appeared in non-avian dinosaurs based on a *Citipati* clutch-adult association from Ukhaa Tolgod, Mongolia. Up to now, five clutch-adult associations have been discovered in China and Mongolia, demonstrating that the clutch-adult association is not an exceptional case (Osborn, 1924; Norell et al., 1995; Dong & Currie, 1996; Webster, 1996; Clark et al., 1999; Norell et al., 2018). However, this hypothesis was questioned by several studies (Martin & Simmons, 1995; Deeming, 2002a; Hopp & Orsen, 2004; Yang, Cheng & Yang, 2011; Jones et al., 2012). All hypotheses are compromised by previous ill-defined interpretations of the clutch architecture of an oviraptorid clutch (Norell et al., 1995; Dong & Currie, 1996; Deeming, 2002a; Fanti, Currie & Badamgarav, 2012; Varricchio & Jackson, 2016). A reevaluation of oviraptorid clutch architecture that includes all available evidence is thus crucial to decipher the reproductive biology of oviraptorids.

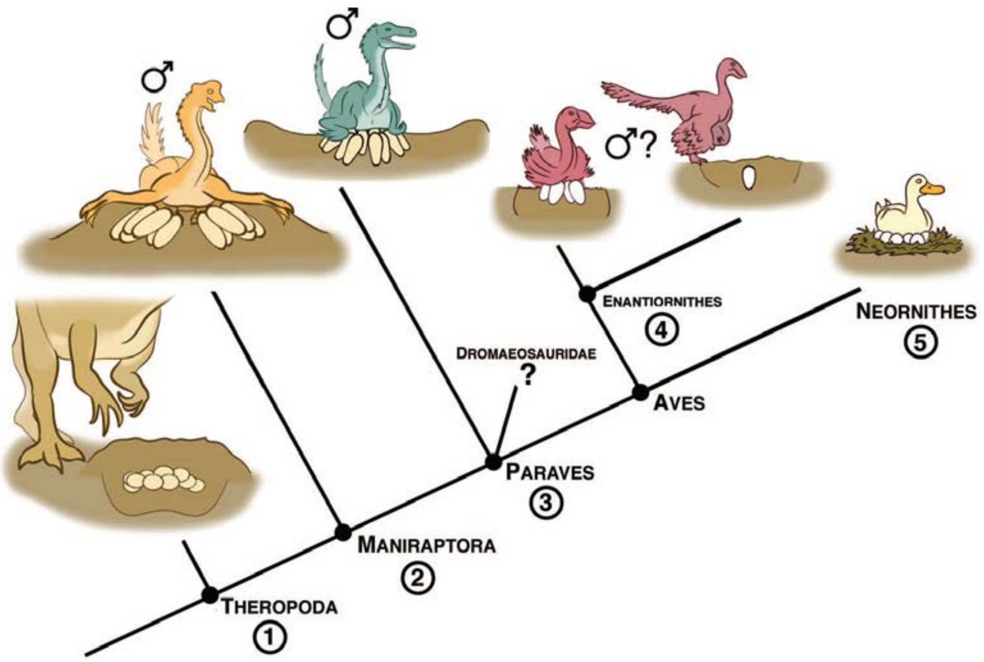

Figure 1-1 Phylogeny with five hypothesized stages for the evolution of reproductive biology from basal theropod to modern birds. Stage 1, basal theropods: spherical eggs with high porosity in a buried nest, neither brooding nor parental care. Stage 2, oviraptors: monoautochronic ovulation, egg size increase, more elongate egg shape, prominent surface ornamentation, male brooding on a clutch of highly organized, paired-arranged eggs in a buried nest. Stage 3, troodontids: monoautochronic ovulation, increasing egg asymmetry, no surface ornamentation, male brooding on a clutch of highly organized, paired-arranged eggs in a partial open nest. Stage 4, Enantiornithes: right ovary and oviduct regress, increasing relative egg size, reduction in egg elongation, possibly brooding on a clutch of eggs or a single egg, buried in sand. Stage 5, Neonithes (modern birds): monochronic ovulation (single oviduct that produces one egg per oviposition). However, the studies in this dissertation indicated that this continuum is problematic since oviraptorosaurs exhibited a peculiar reproductive biology that is not analogous to any extant clades. Reproduced from Varricchio & Jackson (2016).

A number of hypotheses have been proposed regarding reproductive biology of oviraptorids. Sato et al. (2005) reported a gravid oviraptorosaur and suggested that the specimen represents an intermediate stage of oviduct function between reptiles and birds (monoautochronic ovulation, two functional oviducts, each produces one egg per oviposition). This report explained the pairedness in numerous oviraptorosaurian clutches. In recent years, several studies attempted to elucidate reproductive behaviors in oviraptorid dinosaurs. For instance, a report of four oviraptorid embryo-bearing eggs, which were putatively assigned to a single clutch, suggested that oviraptorid dinosaurs hatched asynchronously (Weishampel et al., 2008). In the same year, based on statistical analyses of the ratio of clutch size to adult mass and the absence of medullary bone in the clutch-adult associations, Varricchio et al. (2008) suggested the presence of polygamous behavior in troodontid and oviraptorid dinosaurs. However, Birchard, Ruta & Deeming (2013) applied the statistical methodology in Varricchio et al. (2008) to a bigger dataset, and found that polygamous behavior cannot be inferred from the ratio of clutch size to adult mass in birds. To conclude, all aforementioned pioneer studies on reproductive behaviors of oviraptorid dinosaurs need more supportive evidence or further investigation by means of new techniques.

Varricchio & Jackson (2016) reviewed a surge of studies regarding fossil eggs, embryos, egg clutches, and clutch-adult associations and attempted to conclude a progressive pattern of reproductive biology from (1) basal theropod dinosaurs, (2) oviraptors, (3) troodontids, (4) Enantiornithes, to (5) modern birds (Figure 1-1). They concluded that oviraptors showed intermediate traits in the evolution of reproductive biology between reptiles and modern birds. However, more and more evidence, as shown by various studies in this dissertation, has gradually revealed that oviraptorosaurs exhibited a peculiar reproductive biology that is not analogous to any extant clades, indicating that the evolution of reproductive biology is not a progressive continuum in dinosaurs.

1-3 Aim of Dissertation

The majority of known dinosaur eggs, embryos, and clutches has been ascribed to Oviraptoridae, a subclade of Oviraptorosauria. Although Varricchio & Jackson (2016) have documented and reviewed these fossils and reached several conclusions (see sections 1-1 & 1-2), it has become apparent that more studies are necessary to elucidate the peculiarity of oviraptorid reproductive biology because of sometimes erroneous conclusions of previous authors. Therefore, this dissertation will put emphasis on the reproductive biology of oviraptorid dinosaurs and extend our understanding of their nesting strategies. I hope that this dissertation will amplify the interest in the study of dinosaur eggs because it integrates different biological aspects, chemical analytical methods, and paleontological perspectives to decipher and highlight the distinctiveness of reproduction of oviraptorid dinosaurs.

This dissertation includes an essay, six chapters testing hypotheses, and a synthesis.

The essay (Chapter 2) links reproductive biology to developmental biology to open up a new perspective. Four studies discussing (1) the structure of dinosaur egg and interpreted reproductive biology (Chapter 3 & Chapter 4) and (2) reproduction-related behaviors inferred by new evidence (Chapter 5 & Chapter 6) constitute the core of this dissertation. The Chapter 7 provides a comprehensive synthesis compiled from previous chapters (Chapter 2 to Chapter 6), summarizing our understanding of the reproductive biology of oviraptorid dinosaurs.

1-4 Description of Chapters

Chapter 2, published as Yang & Sander (2018), is an essay inspired by a recent paper about incubation periods in dinosaurs (Erickson et al., 2017). This chapter briefly reviews research on the evolution of bird's beaks and dinosaur incubation periods. Despite of numerous studies on the evolution of bird's toothless beaks from the perspective of developmental biology and ecology, the advantage of bearing a toothless beak is unknown. In this chapter, a new hypothesis, i.e., that the incubation periods may be a selection pressure for toothlessness in birds, is proposed.

Chapter 3, published as Yang et al. (2018a), tests if the cuticle layer, a bi-layered proteinaceous structure covering the calcareous eggshell, is preserved and detectable in fossilized dinosaur eggs. The chapter thus focuses on the preservation of soft tissue in dinosaur eggshells of birds, in an attempt to elucidate the nesting ecology of dinosaurs. While numerous studies showed putative cuticle preservation, all analyses thus far were restricted to observation under the polarized light microscope (PL) or scanning electron microscope (SEM). For the first time, we performed electron probe micro-analysis (EPMA) and Raman spectrometry (RS) on dinosaur eggs and detected the preservation of the cuticle layer. The presence of a cuticle layer suggests an open nesting mode for oviraptorid dinosaurs in the Late Cretaceous mesic environments of southern China.

Chapter 4, published as Wiemann et al. (2017), tests if dinosaur eggs were pigmented using mass spectrometry. *Macroolithus yaotunensis* eggs, assignable to the oviraptorid *Heyuannia huangi* from different Chinese localities were sampled for this study. The chemical analysis suggests that *Heyuannia* eggs were blue-green in color. From an ecological perspective, colored eggs would have been camouflaged *Heyuannia*, reducing egg predation. The study also revealed that oviraptor eggs were semi-buried, based on the heterogeneous distribution of porosity in the *Heyuannia* egg. The discovery of pigmentation in oviraptorid dinosaur eggshells concurred the conclusion in Chapter 3 that oviraptorid dinosaurs built at least partially open nest.

Chapter 5 describes five complete *Macroolithus* clutches from China and re-examines two reported oviraptor clutch-adult associations. Since 1995, the oviraptor adults sitting atop a clutch have been interpreted as brooding behavior in dinosaurs. While several studies argued against the brooding hypothesis, none of them has proposed an alternative hypothesis to explain the occurrence of oviraptor adult-associated specimens. This study integrates ecological and taphonomic aspects to propose that the sitting oviraptorid dinosaurs were not brooding, but in the process of laying. In addition, the oviraptorid nest is reconstructed for the first time based on taphonomic evidence and previous work on the pigment detection and porosity distribution (Chapter 3 & Chapter 4).

Chapter 6 reports a partial oviraptorid embryo-bearing clutch from Hongcheng Basin, Jiangxi, China. This specimen consists of three embryo-bearing eggs, including a pair and a single eggs. The stage of development of the embryos reveals an asynchronous hatching mode for oviraptorids. In accordance with a previous study (Weishampel et al., 2008), this chapter demonstrates that asynchronous hatching is a typical feature of oviraptorids.

Chapter 7 is a comprehensive review that discusses the reproductive biology of oviraptorids, and, more generally, oviraptorosaurians. The origin of the peculiar avian reproductive behavior has long attracted attention of evolutionary biologists and paleontologists. Integrating the results of previous studies, we intend to arrive at a comprehensive hypothesis for oviraptorid reproductive biology, and to extend our understanding from oviraptorid to other clades within Dinosauria. As noted, Varricchio & Jackson (2016) had suggested that oviraptors exhibited an intermediate stage in the evolution toward modern birds. Chapter 7, on the other hand, highlights the peculiar reproductive biology of oviraptors that does represent an intermediate stage between basal dinosaurs and birds.

1-5 Institutional and Technical Abbreviations

Institutional abbreviations: AGM, Anhui Geological Museum, Hefei, Anhui Province, China; CM, Chimei Museum, Tainan, Taiwan; BMNH, Beijing Museum of Natural History, Beijing, China; CMN, Canadian Museum of Nature, Ottawa, Canada; DM, Darwin Museum, Keelung, Taiwan; HGM, Henan Geological Museum, Zhengzhou, Henan Province, China; IGM, Institute of Geology, Ulaanbaatar, Mongolia; IMM, Inner Mongolia Museum, Hohhot, Inner Mongolia Province, China; IMNH, Idaho Museum of Natural History, Pocatello, Idaho, USA; IPB, Institute of Paleontology, Universität Bonn, Bonn, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MNHM, Mokpo Natural History Museum, Mokpo, South Korea; MOR, Museum of the Rockies, Bozeman, Montana, USA; MPC, Mongolian Paleontological Center, Ulaan Baatar, Mongolia; NMNS, National Museum of Natural Sciences, Taichung, Taiwan; MPIE, Max-Planck-Institute for Iron Research, Dusseldorf, Germany; PFMM, Paleowonders Fossil and Mineral Museum, New Taipei City, Taiwan (current name: SMNH, Shishang Museum of Natural History, New Taipei City, Taiwan); SDM, Sihai Dinosaur Popular Science and Culture Museum of Shanghai, Shanghai, China; STM, Shandong Tianyu Museum of Nature, Linyi, Shandong Province, China; XDEM, Xixia Dinosaur Egg Museum, Xixia, Henan Province, China; ZFMK, Forschungsinstitut und Museum Alexander König, Bonn, Germany.

Technical abbreviations: CT-Scan, X-ray computed tomography scan; EPMA, electron probe micro-analysis; ESI-Q-TOF-MS, Electrospray ionization quadrupole time-of-flight mass spectrometry; FEI-SEM, field emission scanning electron microscope; Fm, Formation; HPLC, high performance liquid chromatography; MT, *membrana testacea*; PLM, polarized light microscopy; RS, Raman spectrometry; SEM, scanning electron microscopy; TEM, transmission electron microscopy; WDS, wavelength dispersive spectrometer; ZAF, matrix correction factors. Z, atomic number correction; A, absorption correction; F, characteristic fluorescence correction.

Chapter 2 The origin of the bird's beak: New insights from dinosaur egg incubation periods

PUBLICATION

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(with some modifications)

ABSTRACT

The toothless beak of modern birds was considered as an adaption for feeding ecology; however, several recent studies suggested that developmental factors are also responsible for the toothless beak. Neontological and palaeontological studies have progressively uncovered how birds evolved toothless beaks and suggested that the multiple occurrences of complete edentulism in non-avian dinosaurs were the result of selection for specialized diets. Although developmental biology and ecological factors are not mutually exclusive, the conventional hypothesis that ecological factors account for the toothless beak appears insufficient. A recent study on dinosaur incubation period using embryonic teeth posited that tooth formation rate limits developmental speed, constraining toothed dinosaur incubation to slow reptilian rates. We suggest that selection for tooth loss was a side effect of selection for fast embryo growth and thus shorter incubation. This observation would also explain the multiple occurrences of tooth loss and beaks in non-avian dinosaur taxa crownward of *Tyrannosaurus*. Whereas our hypothesis is an observation without any experimental supports, more studies of gene regulation of tooth formation in embryos would allow testing for the trade-off between incubation period and tooth development.

2-1 Introduction

As often in evolutionary research, a comprehensive perspective that includes life forms only known from the fossil record helps to decide between alternative hypotheses that were established only based on the living survivors. Theropod dinosaurs crownward of Tyrannosaurus evolved smaller body sizes approaching those of birds and varied feeding preferences, particularly in near-bird dinosaurs (Lautenschlager et al., 2013; Lee et al., 2014). Some were even herbivorous and beaked in the bird sense (toothless and with a rhamphotheca).

While such beaks are also present in turtles and some extinct reptile clades, birds are the most diverse and arguably most successful beaked amniote clade. The beak is one of many other characters (prime among them are feathers; Koschowitz, Fischer & Sander, 2014; Xu et al., 2014) once considered unique to birds and a pivotal innovation, which enabled birds to survive through the K-Pg extinction event (Larson, Brown & Evans, 2016). The origin of the beak has been ascribed to both genetic (developmental economy) and ecological (food acquisition and flights) causes in the recent literature (Lautenschlager et al., 2013; Bhullar et al., 2015; Bhullar et al., 2016; Bright et al., 2016; Cooney et al., 2017; Felice & Goswami, 2017; Wang et al., 2017a; Wang et al., 2017b; Wang, Zhang & Yang, 2018). Based on a recent elegant study of dinosaur embryonic teeth (Erickson et al., 2017), we hypothesized that incubation period is a key selection pressure for toothlessness.

2-2 The Conventional Hypothesis for the Origin of Edentulism and the Beak

Numerous toothless non-avian dinosaurs and toothed Mesozoic birds (e.g., *Hesperornis* and *Ichthyornis*) reveal that edentulism evolved several times in dinosaurs (Figure 2-1). Zhou, Zhang & Li (2010) assumed that birds lost their teeth for a reduction in body weight and active flight; however, this hypothesis is invalidated by numerous discoveries of airborne toothed Mesozoic birds such as pelagornithids and *Ichthyornis*. The conventional hypothesis for the origin of birds' toothless beak attributes this feature to ecological adaptations (Zusi, 1993), and a surge of recent studies appears to provide support (Hieronymus & Witmer, 2010; Zanno & Makovicky, 2011; Larson, Brown & Evans, 2016; Cooney et al., 2017). For instance, Cooney et al. (2017) showed that ecological adaption led to the explosive diversification of bird's beaks after the mass extinction at the end of the Cretaceous, 66 million years ago. However, the K-Pg mass extinction event also wiped out some edentulous Mesozoic birds, indicating that ecological factors cannot be the only explanation (Larson, Brown & Evans, 2016). Alternatively, edentulism and the beak have been hypothesized to strengthen the skull of some non-avian theropods and birds (Lautenschlager et al., 2013), but hypotheses rooted in development also have to be considered. The morphometric studies of Bright et al. (2016) on living raptors and Felice & Goswami (2017) indicated that bird beak shape is strongly coupled with body size and controlled by nondietary factors such as specific genes active during development. They also hypothesized that non-avian dinosaurs and birds faced similar constraints on beak shape and broke the developmental constraint to vary their beak shape.

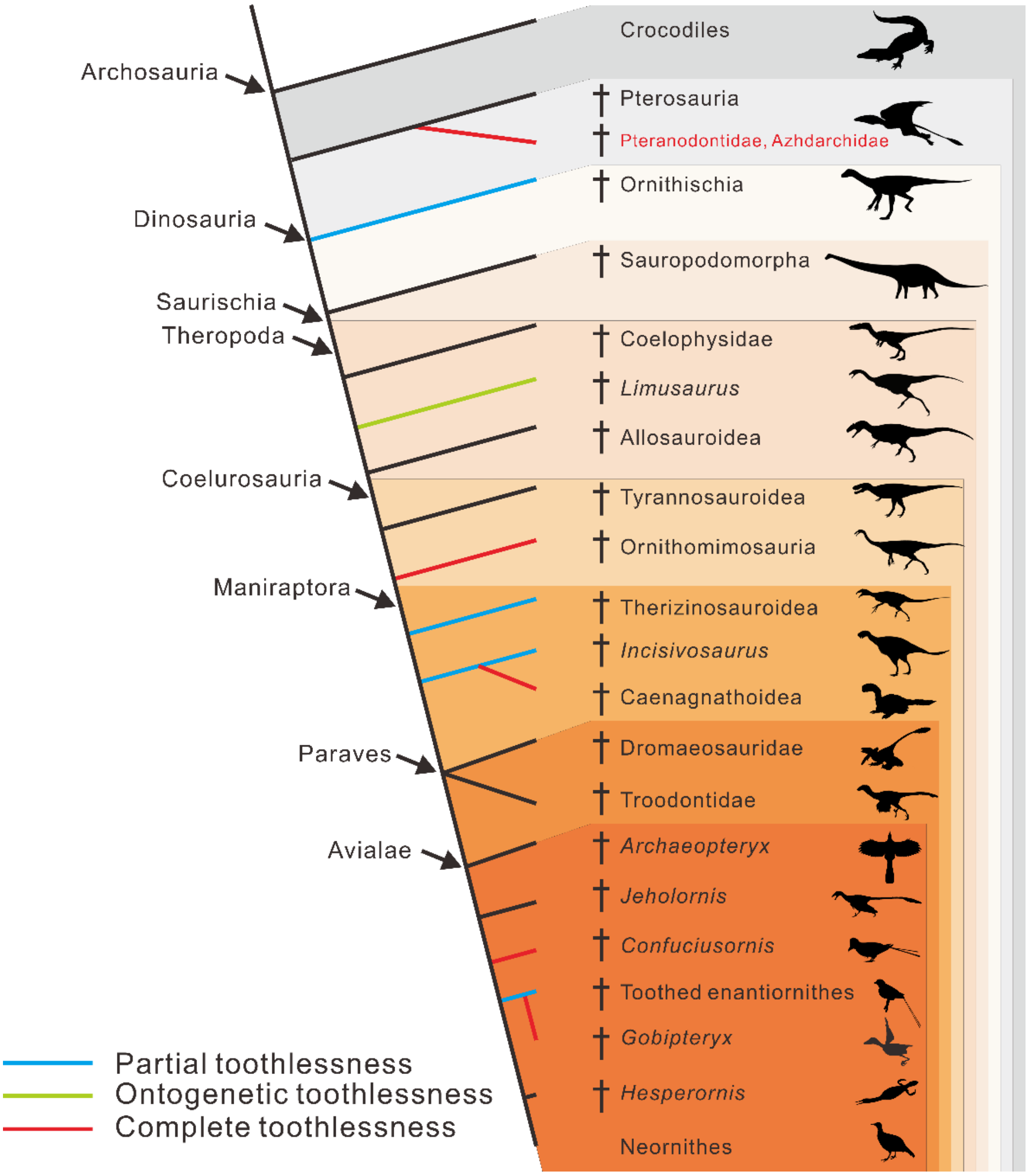

Figure 2-1 Toothlessness in dinosaurs. Consensus cladogram of Archosauria shows that edentulism frequently evolved independently in several lineages. All Ornithischia, Therizinosauroidea, *Incisivosaurus*, and toothed Enantiornithes exhibit partial tooth loss. Ontogenetic edentulism has been reported for the theropod *Limusaurus* from China (Wang et al., 2017a). Complete edentulism is observed in some pterosaurs, Ornithomimosauria, Caenagnathoidea (including Oviraptoridae), some Mesozoic birds such as *Confuciusornis* and *Gobipteryx*, and all extant birds (Neornithes). Silhouettes were taken from public domain images on phylopic.org.

2-3 Developmental Evidence from Genetics and Fossils

Numerous studies from developmental biology have proposed various genetic mechanisms to explain edentulism. Chen et al. (2000) provided evidence for edentulism involving a mutation that inactivated the genetic pathways for tooth formation in deep evolutionary history. In fact, birds still retain some intact signalling pathways for tooth formation, consistent with the existence of tooth primordia (Chen et al., 2000). Chen et al. (2000)'s developmental biology experiments suggested that the absence of Bmp4 contributes to edentulism in the chicken. In another study, Harris et al. (2006) hypothesized that the loss of direct apposition between an epithelial signalling centre and the mesenchyme is responsible for avian edentulism.

Combining evidence from fossils and experimental developmental biology revealed the genetic regulation of edentulism in modern birds and provided a potential genetic mechanism for its evolution (Bhullar et al., 2015; Bhullar et al., 2016). A developmental explanation for the origin of edentulism was further supported by three very recent studies based on fossils: one on the Jurassic ceratosaurian theropod *Limusaurus* (Wang et al., 2017a) and the other two on a caenagnathid oviraptorosaur (Figure 2-2; Wang et al., 2017b; Wang, Zhang & Yang, 2018) and the Early Cretaceous bird *Sapeornis* (Figure 2-2; Wang et al., 2017b). *Limusaurus* gradually lost teeth with age, indicating that its edentulism evolved through a shift toward earlier cessation of tooth replacement, which can be explained by heterochrony, specifically progenesis (Figure 2-3; Wang et al., 2017b). The studies on the caenagnathid and *Sapeornis* supported this interpretation of heterochrony (Wang et al., 2017a; Wang, Zhang & Yang, 2018).

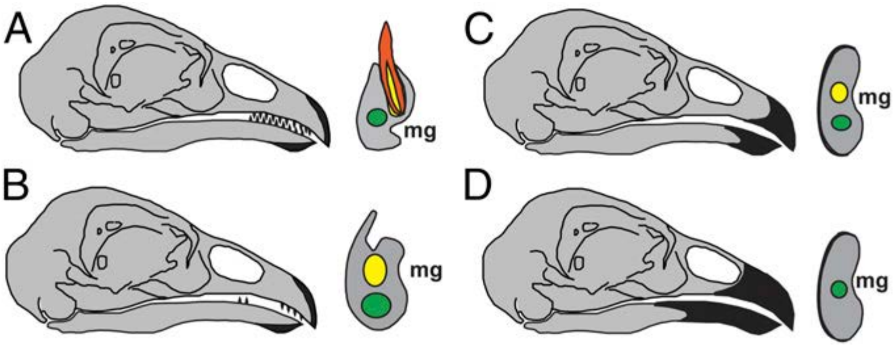

Figure 2-2 A model of therapod toothlessness. Right lateral view of skull (left) and transverse view of dentary (right) (reprinted from Wang et al., 2017b). (A) Normal tooth development without being hampered by the rhamphotheca (grey part). (B) Tooth growth is hampered by the closure of alveoli. (C) Remaining teeth malfunctioned when the rhamphotheca expands. (D) Toothless beak covered by rhamphotheca. Green, mandibular canal; yellow, alveolus and alveolar canal; orange, tooth; grey, rhamphotheca. (Not to scale)

2-4 Incubation Periods as a Selective Factor for Edentulism

Support for the importance of heterochrony in beak evolution now comes from an unexpected line of evidence, reproductive biology of non-avian dinosaurs. Once believed to be inaccessible in fossils, data on dinosaur incubation periods have become available by an ever-increasing sample of dinosaur embryos preserved at different stages of development. This unexpected line of evidence is brought to bear in an elegant new study based on such fossils by Erickson et al. (2017).

All dinosaurs hatched from eggs, and incubation period is one of the crucial traits in reproductive biology of egg-laying (oviparous) amniotes. Incubation time is of great evolutionary significance (Werner & Griebeler, 2013; Ruxton, Birchard & Deeming, 2014; Erickson et al., 2017). Fast incubation reduces the risk of egg mortality from predation, diseases, and natural disasters. In the past, dinosaur incubation periods were estimated using bird models as 45 to 82 days, but Erickson et al. (2017) now provide direct evidence to the contrary. This evidence is von Ebner lines (daily incremental lines in tooth dentin) in embryonic teeth of two groups of ornithischian dinosaurs, ceratopsians and hadrosaurids. Von Ebner line counts in Late Cretaceous *Protoceratops* embryos from Mongolia and *Hypacrosaurus* embryos from Canada indicate that these dinosaurs had the long incubation periods of three to six month typical of modern reptiles.

Since there is a great selective advantage to fast incubation and to fast development in general, this raises the question of what limited incubation period in these ceratopsians and hadrosaurs to slow reptilian rates and how this limitation was overcome in derived theropods, i.e., on the line to modern birds. Erickson et al. (2017) hypothesized the rate of tooth dentin formation in the embryo to be the limiting factor. They note that teeth do not appear earlier than around 40% through incubation time, and that tooth formation rate is constrained by the maximum thickness of 30 μm of the daily growth increments in the dentin (von Ebner lines). The authors posit accordingly that all toothed dinosaurs would have been restricted to long reptilian incubation periods.

This hypothesis is consistent with the observation that most dinosaurs built reptile-like nests by burying their eggs and providing little parental care (Varricchio & Jackson, 2016). Only in dinosaurs crownward of *Tyrannosaurus* is there evidence for the evolution of open nests and brooding, which would have made faster incubation possible than in buried eggs (Figure 2-1; Deeming et al., 2006; Varricchio & Jackson, 2016). Evidence for brooding goes along with evidence for endothermy such as fast growth (Erickson, 2014) and insulation (Koschowitz, Fischer & Sander, 2014). If Erickson et al. (2017) are correct, selection pressure for fast incubation would favour tooth loss and would explain the multiple evolution of beaks in non-avian dinosaurs crownward of *Tyrannosaurus*. The selection pressure for fast incubation also acted in early birds (Figure 2-1) and is consistent with the slow development of the toothed urvogel *Archaeopteryx* (Xu et al., 2014).

However, independently of dinosaurs and modern birds, edentulism and a horny beak evolved in several other amniote lineages, such as turtles, some marine reptiles and pterosaurs. Turtles retain a long incubation period, approximately 42-112 days (Deeming et al., 2006) which seemingly contradicts our hypothesis that edentulism results from selection for a shorter incubation period. This contradiction is also presented by megapode birds that have long incubation times and bury their eggs, yet it is generally agreed that megapode nesting biology is secondarily derived instead of being inherited from non-avian dinosaurs (Dekker, 2007). Given that the evolution of edentulism is a complex process, these contradictions suggest the influence of other constraints, some of which may be phylogenetic. This is hinted at by the new study of Baron, Norman & Barrett (2017) which challenges dogma and re-divides dinosaurs into Ornithoscelida and Saurischia, doing away with the canonical Saurischia-Ornithischia dichotomy. As newly defined, Saurischia no longer includes theropods, but the Theropoda (excluding Herrerasauridae) and Ornithischia form a clade Ornithoscelida. All Ornithischia have beaks, but always in combination with teeth, as do some theropods. Among dinosaurs, beaks would be thus further restricted to a subclade of Dinosauria, the Ornithoscelida. Alternatively, the ability to evolve a beak may characterize a much more inclusive clade because some derived pterosaurs possessed edentulous beaks and no longer appear randomly distributed among dinosaurs and it was recently suggested that sauropod dinosaurs also had a type of beak (Wiersma & Sander, 2017).

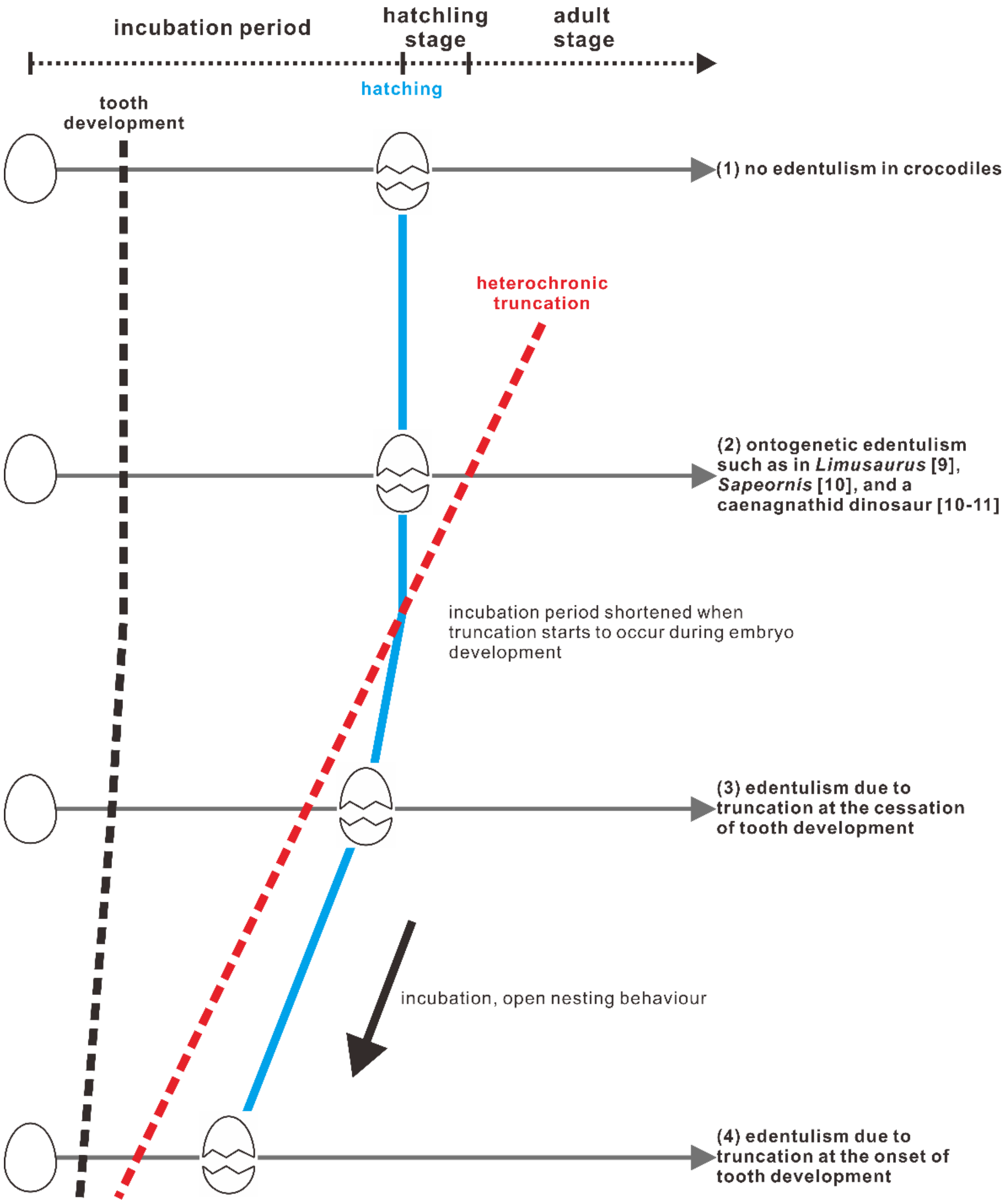

Figure 2-3 Schematic illustration of the hypothetical four stages of the evolution of edentulism. Stage 1, neither edentulism nor heterochronic truncation of tooth formation. Stage 2, ontogenetic edentulism, heterochronic truncation of tooth replacement occurs after the eruption of functional generations of teeth. Stage 3, complete edentulism, heterochronic truncation occurs at the cessation of embryonic tooth formation. Stage 4, complete edentulism, the heterochronic truncation occurs at the onset of embryonic tooth formation, as indicated by the existence of tooth primordia in modern birds (Chen et al., 2000).

2-5 Potential Tests of Hypotheses of Developmental Economy

Reproductive biological factors, as suggested by our hypothesis, represent an improvement in developmental economy for the evolution of edentulism called for in an earlier review (Louchart & Viriot, 2011). A preliminary report by Varricchio, Kundrat & Hogan (2017) on *Troodon* embryonic teeth inferred an incubation period of 74 days , which is much shorter than the 113.93 days predicted for a reptilian egg of the same mass but significantly longer than the 49.01 days for a bird egg of the same mass (Deeming et al., 2006). Such an intermediate incubation period, in between the slow reptilian and fast avian modes, was possibly determined by the interplay of tooth formation and an extensive parental care (Varricchio et al., 1997), which lends support to our hypothesis. It is hence crucial to investigate if edentulous fossil taxa exhibited accelerated incubation and if toothed basal birds had long incubation periods.

Apart from allometric analyses (Werner & Griebeler, 2013; Ruxton, Birchard & Deeming, 2014), counting growth marks in embryonic teeth is currently the only method for estimating incubation periods in fossil taxa (Erickson et al., 2017; Varricchio, Kundrat & Hogan, 2017); however, this method obviously cannot be applied to those edentulous fossil taxa. Experimental evo-devo research, such as inhibiting specific genes responsible for tooth formation, may inform on the influence of toothlessness on incubation periods (Chen et al., 2000; Harris et al., 2006; Bhullar et al., 2015; Bhullar et al., 2016).

In addition to ecological factors, our hypothesis explains the observation of multiple appearances of edentulism and highlights a new selective advantage of edentulism, i.e., improving developmental economy and accelerating incubation periods. Developmental and reproductive biology thus play an important role in influencing many features such as the beak and feathers that were previously explained by feeding preferences and flight, respectively.

Chapter 3 Fossil Eggshell Cuticle Elucidates Dinosaur Nesting Ecology

PUBLICATION

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ABSTRACT

The cuticle layer consisting mainly of lipids and hydroxyapatite (HAp) atop the mineralized avian eggshell is a protective structure that prevents the egg from dehydration and microbial invasions. Previous ornithological studies have revealed that the cuticle layer is also involved in modulating the reflectance of eggshells in addition to pigments (protoporphyrin and biliverdin). Thus, the cuticle layer represents a crucial trait that delivers ecological signals. While present in most modern birds, direct evidence for cuticle preservation in stem birds and non-avian dinosaurs is yet missing. Here we present the first direct and chemical evidence for the preservation of the cuticle layer on dinosaur eggshells. We analyze several theropod eggshells from various localities, including oviraptorid *Macroolithus yaotunensis* eggshells from the Late Cretaceous deposits of Henan, Jiangxi, and Guangdong in China and alvarezsaurid *Triprismatoolithus* eggshell from the Two Medicine Formation of Montana, United States, with the scanning electron microscope (SEM), electron probe micro-analysis (EPMA), and Raman spectroscopy (RS). The elemental analysis with EPMA shows high concentration of phosphorus at the boundary between the eggshell and sediment, representing the hydroxyapatitic cuticle layer (HAp). Depletion of phosphorus in sediment excludes the allochthonous origin of the phosphorus in these eggshells. The chemometric analysis of Raman spectra collected from fossil and extant eggs provides further supportive evidence for the cuticle preservation in oviraptorid and probable alvarezsaurid eggshells. In accordance

with our previous discovery of pigments preserved in Cretaceous oviraptorid dinosaur eggshells, we validate the cuticle preservation on dinosaur eggshells through deep time and offer a yet unexplored resource for chemical studies targeting the evolution of dinosaur nesting ecology. Our study also suggests that the cuticle structure can be traced far back to maniraptoran dinosaurs and enhance their reproductive success in a warm and mesic habitat such as Montana and southern China during the Late Cretaceous.

3-1 Introduction

3-1-1 Cuticle Structures and Functions

An avian egg is an evolutionary invention that protects the developing embryo against mechanical damage, dehydration and microbial invasion (Romanoff & Romanoff, 1949; Board & Fuller, 1974). This multi-functionality is contributed to by both mineralized and non-mineralized, organic layers, which exhibit unique biomaterial properties. The avian eggshell forms inside the uterus. The final layer to be deposited, the eggshell cuticle, represents the interface between the embryo inside and its outside environment. Many bird eggs are equipped with a cuticle layer; however, this structure is absent in some clades such as parrots, petrels, and pigeons (D'Alba et al., 2016). The cuticle layer is often described as "waxy" due to its high amount of lipids, which keep the internal fluids from evaporating and therefore protect the encased embryo from desiccation. In addition to lipids, the avian cuticle contains proteins, polysaccharides, calcium carbonate (vaterite), calcium phosphates (hydroxyapatite, HAp), and pigments (Wedral, Vadehra & Baker, 1974; Nys et al., 1991; Packard & DeMarco, 1991; Dennis et al., 1996; Mikhailov & Ornithologists' Club, 1997; Fraser, Bain & Solomon, 1999; Cusack, Fraser & Stachel, 2003; Igic et al., 2015).

The cuticle layer varies in thickness (up to 12µm) and has a patchy distribution on the eggshell (Board & Halls, 1973). Basically, the cuticle is divided into two distinct layers, including an amorphous HAp/vaterite inner layer and a proteinaceous outer layer (Simons, 1971; Dennis et al., 1996; Fraser, Bain & Solomon, 1999). The inner cuticle layer is composed of needle-like HAp/vaterite crystals on some avian eggs but present in the form of nanospherical HAp/vaterite on other avian eggs (Dennis et al., 1996; D'Alba et al., 2014). A recent study suggested that the circular mineral nanospheres on eggshells serve an antimicrobial function for species nesting in humid environment (D'Alba et al., 2016). D'Alba et al. (2016) also proposed that eggs in humid environments tend to have more cuticular nanospheres to prevent flooding and microbial invasions. Conversely, in arid environments, lacking a cuticle layer would be beneficial for embryos in eggs with low conductance, as Deeming (1987) suggested. However, in an extreme environment such as the Antarctic, Adélie penguin eggs yield a thick cuticle layer to reduce water loss

(Thompson & Goldie, 1990). Besides, the intactness of the cuticle is an indicator for the freshness of an egg (Rodríguez-Navarro et al., 2013). Several studies suggested that the cuticle functions as a lubricant that facilitates egg rotation in the uterus (Rahman et al., 2009). Moreover, a recent study shows that the cuticle also modulates ultraviolet reflectance of avian eggshells (Fecheyr-Lippens et al., 2015). For instance, an extremely smooth cuticle produces glossiness and iridescence in tinamou eggs (Igic et al., 2015).

The cuticle is commonly observed on most calcified eggshells, but it shows different structures and characteristics between reptilian and avian eggshells (Ferguson, 1982). The cuticle on reptilian eggshells is no longer present after two weeks of laying (Ferguson, 1982); hence, the author concluded that the reptilian cuticle is not equivalent to the cuticle present on avian eggshells. Ferguson (1982) hypothesized that a true cuticle layer is not present on alligator eggshell. Conversely, avian eggshells exhibit an inner cuticle layer composed of HAp/vaterite granules or amorphous needle-like HAp/vaterite crystals, which are absent on reptilian eggshells. Several studies on extant eggshell have identified cuticle presence by means of the scanning electron microscopy (SEM) and transmission electron microscopy (TEM) (Fink et al., 1993; Fraser, Bain & Solomon, 1999). Kusuda et al. (2011) used energy dispersive X-ray analysis (EDX) to map the phosphorus (P) and calcium (Ca) distribution in several extant avian eggshells and discovered that P is confined to the cuticle layer. Although the P concentration in the cuticle varies greatly between different bird species, P is a distinct marker for identifying the cuticle layer in case of P depletion in sediment. Although it is still not clear how P functions during the eggshell formation, a study suggested that the inclusion of P in the biomineral terminates eggshell growth since it competes with calcium during the eggshell crystallization (Cusack, Fraser & Stachel, 2003).

3-1-2 Discoveries of Fossilized Organic Membranes

Since the cuticle is composed of proteins, polysaccharides, lipids, calcium carbonate, calcium phosphates, and pigments, it is seemingly unlikely to preserve during the fossilization process. A previous report concerning spherical (*Oölithus spheroides*) and elongated (*Oölithus elongatus*) eggs from Laiyang, Shandong, China, suggested that the cuticle is preserved in elongated eggs but not in spherical ones (Chow, 1954). Another similar report on ornithoid eggshells from Naran-Bulak, Mongolia also described possible cuticle preservations (Sochava, 1971), but no diagnostic chemical data were obtained. Kohring & Hirsch (1996) studied the crocodilian and ornithoid eggshells from the middle Eocene of the Geiseltal, Germany, and suggested possible cuticle and shell membrane preservation. Later, with the SEM, several studies on dinosaur eggshells, Cretaceous bird eggshells, and fossil moa eggshells showed the potential of cuticle preservation (Mikhailov, 1991; Varricchio & Jackson, 2004; Jackson & Varricchio, 2010; Oskam et al., 2010). Although these studies provided a new avenue to understanding soft-part preservation, all previous studies described possible cuticle preservation only based on micro-structural comparisons with the cuticle of extant avian eggshells. Jackson & Varricchio (2010) described a new ootaxon – *Triprismatoolithus stephensi* – of probable alvarezsaurid affinities. These authors reported a cracked and amorphous surface overlying the external layer and suggested it might be a layer of cuticle. Nevertheless, they did not further investigate the possible cuticle layer by means of any other analyses. Therefore, all previous reports regarding the cuticle preservation were constrained to micro-morphological observations. The only chemical evidence supporting the fossilization potential of cuticle through deep time is offered by a study on oviraptorid eggshells focusing on the two main eggshell pigments, biliverdin and protoporphyrin (Wiemann et al., 2017). The protoporphyrin is deposited predominantly in the cuticle layer (Schwartz et al., 1975; Nys et al., 1991; Mikšík et al., 2007; Nys & Guyot, 2011), thus providing indirect evidence of cuticle preservation in the preservation of endogenous protoporphyrin (Wiemann et al., 2017). Although Wilson et al. (2017) demonstrated that there is no codependence of the deposition of pigment and cuticle, the preserved pigments in the oviraptorid eggshell could derive from the eggshell or the preserved cuticle layer and in the latter instance would be indicative of cuticle preservation. We hence posited that the cuticle was completely, or partially, preserved on the oviraptorid eggshells. In addition to the cuticle layer, the *membrana testacea* (eggshell membranes), a proteinaceous meshwork that underlies the mineralized eggshell and separates egg yolk and eggshell, is also a crucial membrane. Unlike the cuticle layer, the preservation of *membrana testacea* has been reported from titanosaurid and *Lufengosaurus* eggs (Grellet-Tinner, 2005; Reisz et al., 2013), yet never in theropod eggs.

3-1-3 Nesting Ecology of Dinosaurs and Modern Birds

Dinosaur nesting ecology is a long-standing and intriguing research topic. Among all dinosaurs, the nesting type of titanosaur, troodontid, and oviraptorid dinosaurs were comparatively well documented (Jackson, 2007; Varricchio et al., 2013; Wiemann et al., 2017). These dinosaurs adopted different nesting strategies in their clutch arrangement, nest architecture, and nesting mode. Deeming (2006) and Tanaka, Zelenitsky & Therrien (2015) roughly categorized two nesting modes in dinosaurs, including open and buried nesting modes. Most birds build open nests, while the buried nesting mode is only observed in megapode birds. In a wet incubation environment such as a buried megapode nest, eggs are exposed to a higher risk of asphyxiation and microbial infection (Board & Fuller, 1974; Board, 1982; D'Alba et al., 2017). D'Alba et al. (2016) provided the first report regarding the association between the cuticular nanospheres and nesting modes. These authors discovered that the birds nesting in more mesic environments tend to lay eggs yielding cuticular nanospheres. The nanospheres in the cuticle layer, therefore, represents a structural adaptation that prevents eggs from microbial invasions (D'Alba et al., 2016). However, eggs of Adélie penguins are also encapsulated by a thick cuticle layer that prevents eggs from water loss in the severe cold Antarctic environment (Thompson & Goldie, 1990). These lines of evidence suggest that the cuticle layer is an evolutionary labile structure and thus varies greatly in accordance with the nesting environment. D'Alba et al. (2016) further suggested that cuticular nanospheres are an ancestral trait; however, this trait has been lost multiple times and is absent in some avian clades.

In dinosaurs, it was suggested that titanosaurs also employed the buried nesting mode (Sander et al., 1998; Sander et al., 2008; Grellet-Tinner & Fiorelli, 2010; Vila et al., 2010; Hechenleitner, Grellet-Tinner & Fiorelli, 2015). The low porosity of titanosaur eggs from Auca Mahuevo, however, suggested that the titanosaurs from Auca Mahuevo did not bury their eggs (Jackson, 2007; Sander et al., 2008). The Auca Mahuevo exception demonstrates that the eggshell is a labile structure, which alters according to the environment. In comparison with the well-documented titanosaur nesting ecology, the nesting ecology of theropods has remained uncertain until recent times. A nesting *Nemegtomaia* discovered in Mongolia indicated a semi-open nesting mode based on sedimentological evidence (Fanti, Currie & Badamgarav, 2012). The discovery of pigmentation in oviraptorid eggshells strongly suggested that the oviraptorid eggs were laid in an at least partially open nest (Wiemann et al., 2017). Yang et al. (2015) further supported the semi-open nesting mode according to the heterogeneous distribution of porosity in an oviraptorid egg and taphonomic evidence (also see Wiemann et al., 2017). While there is no evidence of pigmentation in troodontid eggshells because these have not been analyzed chemically so far, the heterogeneous distribution of porosity suggested that the troodontid dinosaurs might also have laid their eggs in a semi-open nest (Varricchio et al., 1997; Varricchio et al., 2013).

The goal of this study is to present further evidence of cuticle preservation on dinosaur eggshells by means of SEM imaging, elemental analysis, and RS. In particular, we analyzed theropod eggshells from the Nanxiong Group in China and the Two Medicine Formation in Montana, USA. Both the Nanxiong Group and Two Medicine Formation represent fluvial deposits, indicating a humid climate in both areas during the Late Cretaceous. In addition, nesting on the ground or in mounds in a wet environment increases the risk of microbial invasions (D'Alba et al., 2016), a cuticle layer should thus be prevalent on eggshells of ground nesting theropods in a humid climate.

3-2 Material and Methods

3-2-1 Material

In order to standardize our following analyses, domestic chicken eggshell (*Gallus gallus domesticus*) was obtained from a commercial source (supermarket). Two extant crocodilian eggshells (*Crocodylus porosus* and *Tomistoma schlegelii*) were sampled from the collection of the NMNS as negative controls (Table 3-1). The fossil materials include oviraptorid and probable alvarezsaurid dinosaur eggshells (Table 3-1).

We studied three oviraptorid eggshell specimens that were collected from the Late Cretaceous Nanxiong Group of three localities in China (Henan Province, Jiangxi Province, and Guangdong Province) and are housed at the NMNS and STIPB. Based on eggshell microstructure, all specimens were assignable to *Macroolithus yaotunensis*, which was laid by the oviraptorid *Heyuannia huangi* (Cheng et al., 2008). *Macroolithus yaotunensis* is characterized by an undulating boundary between two crystalline layers, i.e., the outer prismatic layer and the inner mammillary layer (Zhao, 1975). The first *Macroolithus* *yaotunensis* eggshell was taken from specimen NMNS CYN-2004-DINO-05-I, which was collected from the Late Cretaceous Tangbian Formation of the Hongcheng Basin in Jiangxi Province, China (Table 3-1). The Tangbian Formation is characterized by fine-grained brownish-reddish sediments with dispersed coarse clasts and conglomerates, representing a fluvial/alluvial environment with occasional stream flooding during the Campanian stage (Chen et al., 2017). The second *Macroolithus yaotunensis* sample was collected as isolated shell fragments from the Late Cretaceous Hugang Formation in the Liguanqiao Basin near Nanyang, southwestern Henan Province, China (Table 3-1). This sample has been housed in STIPB since 1985 and was described in Erben (1995). The Hugang Formation is composed of dark grayish red breccia with interbeds of calcareous sandstone, indicating a fluvial/alluvial environment (Zhang, 2009). The third *Macroolithus yaotunensis* sample was also obtained as isolated shell fragments from the Late Cretaceous fluvial deposits of the Pingling Section of the Shanghu Formation in the Nanxiong Basin, located in the northwestern part of Guangdong Province, China (Table 3-1). The NE-SW striking Nanxiong Basin, which is filled with dark purplish silty mudstone with interbeds of conglomerate, has produced numerous theropod egg clutches and eggshell fragments (Erben, 1995).

The *Triprismatoolithus stephensi* eggshells (MOR ES101), probably attributable to alvarezsaurids (Agnolin et al., 2012; Varricchio & Jackson, 2016), were collected as isolated shell fragments in the lower portion of the Two Medicine Formation in the Sevenmile Hill outcrops, Teton County, Montana, USA (Table 3-1). The *Triprismatoolithus stephensi* eggshell has three crystalline layers, including an external layer, prismatic layer, and mammillary layer, from outermost to innermost (Varricchio & Jackson, 2016). The Two Medicine Formation is mostly composed of sandstone, deposited by rivers and deltas on the western shoreline of the Late Cretaceous Interior Seaway.

Table 3-1 Eggshells analyzed in this study.

Oospecies or species	Stratigraphy	Locality	Catalog number	Reference
Macroolithus yaotunensis	Tangbian Formation	Hongcheng Basin, Jiangxi Province, China	NMNS CYN-2004-DINO-05-I	Wiemann et al. (2017)
Macroolithus yaotunensis	Hugang Formation	Liquanqiao Basin, Henan Province, China	STIPB-E131	Wiemann et al. (2017)
Macroolithus yaotunensis	Pingling Formation	Nanxiong Basin, Guangdong Province, China	STIPB-E66	Wiemann et al. (2017)
Triprismatoolithus stephensi	Lower portion of the Upper Cretaceous (Campanian) Two Medicine Formation	Dave and Joel Site, Sevenmile Hill outcrops, Teton County, Montana	MOR ES101	Jackson & Varricchio (2010)
Gallus gallus	-	Bonn, Germany	-	-
Crocodylus porosus	-	Taichung, Taiwan	uncatalogued	-
Tomistoma schlegelii	-	Taichung, Taiwan	uncatalogued	-

3-2-2 Chemical Analyses

For the chemical analyses, we first used a VEGA TS5130 LM (Tescan) SEM at the STIPB to locate and image plausible cuticle preservation on the studied eggshells. The eggshells were naturally broken fragments and coated with gold for SEM observation. The operating conditions for the SEM were set as 20 kV accelerating voltage.

All samples were cleaned with ethanol before chemical analyses. We then performed elemental analyses using the EPMA equipped with a WDS at the Section of Mineralogy of the STIPB to elucidate the P distribution in the radial section of dinosaur eggshells. All samples were polished, fixed on a glass slide with araldite histological resin, and then coated with carbon for the elemental analysis with EPMA. The elemental analyses were performed with a JEOL SUPERPROBE 8900 EPMA at the same lab. The operating conditions for the EPMA were set as 1 μm beam diameter, 15 kV accelerating voltage, and 15 nA specimen current. The ZAF correction scheme was used. Natural and synthetic minerals were used as standards.

We performed two rounds of RS using two Raman spectrometers at the MPIE, Dusseldorf, Germany. For the first round, Raman Analysis I (referred to as RI hereafter), we analyzed the domestic chicken eggshell from a commercial source with a WITec Alpha300 system with 532 nm wavelength laser light and a confocal 50x objective, each for 20 seconds. Since the cuticle on the chicken eggshell was easily identified with the naked eye, as well as under the SEM (Figure 3-1C-D), the first round confirmed the detectability by Raman spectroscopy of the HAp of the cuticle layer (Figure 3-1E-F). Due to the incomplete preservation the cuticle on the chicken eggshell, we performed Raman surface mapping on the area where we found possible cuticle remains using the SEM and EPMA previously.

Raman analysis II (referred to as RII hereinafter) was performed using the Horiba Jobin Yvon GmbH LabRam Raman spectrometer equipped with a 632 nm laser. All results were obtained using the 10x objective of the integrated Olympus microscope. While the 10x objective is not strongly sensitive to rare compounds, it provides a larger field of view for faster qualitative detection of HAp on eggshell sample than in RI. In order to distinguish HAp and calcite from sediments, we collected Raman spectra of the fresh chicken eggshell, the studied fossil eggshells and their associated sediments (Figure 3-2A). All Raman spectra of eggshells and their associated sediments during RII were imported into the statistics software R and normalized with the R package "ChemoSpec" (Hanson, 2017). We performed principle component analysis (PCA) on the spectral area of 500 to 1500 cm^{-1} using the same package (Figure 3-2B).

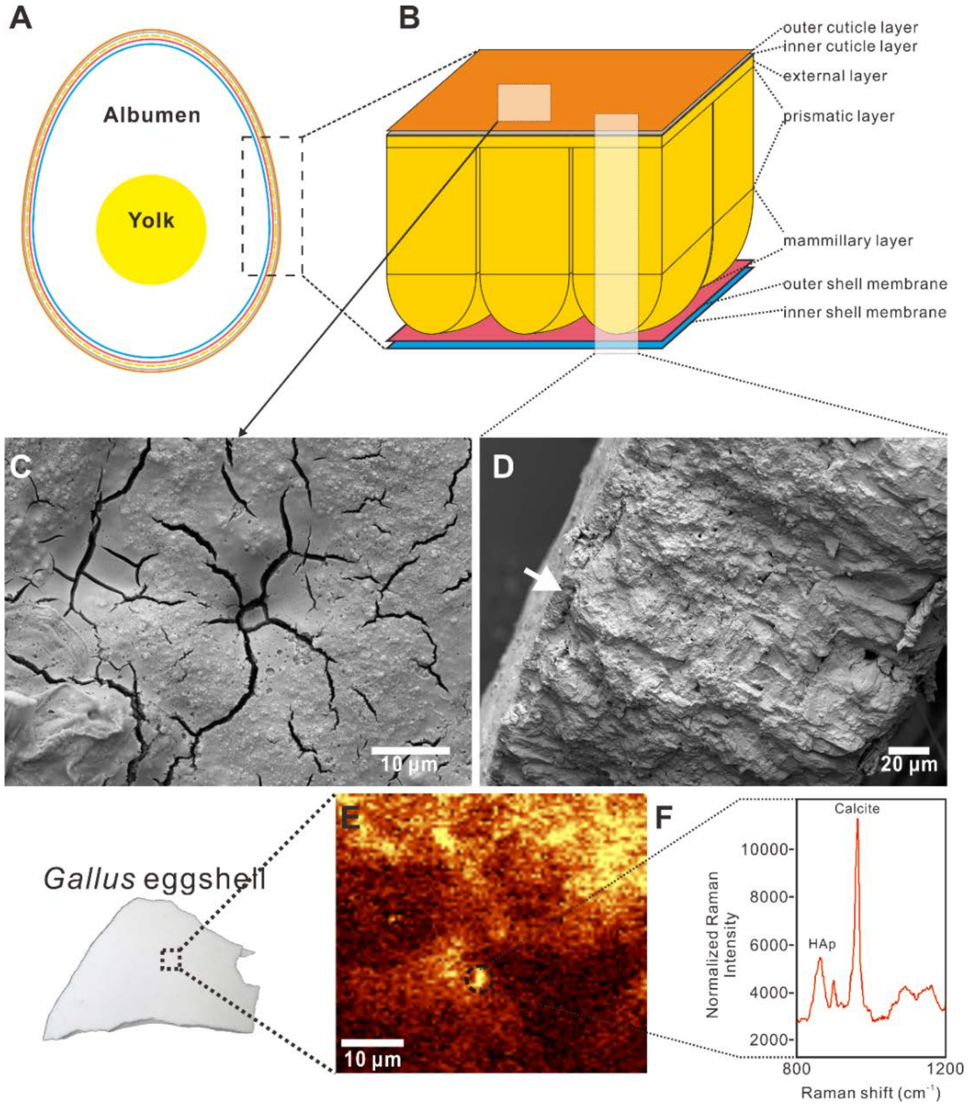


Figure 3-1 Cross-sectional view, SEM images, and Raman imaging and spectrum of a *Gallus gallus domesticus* egg and eggshell. The Raman image and spectrum were collected using 532 nm excitation wavelength and a 50x objective with RI. (A) The generalized anatomy of an egg. (B) The chicken eggshell comprises three crystalline layers, including the mammillary layer, prismatic layer, and external layer. The cuticle layer overlying the calcareous eggshell is further divided to two layers, including a HAp inner layer and a proteinaceous outer layer. The shell membrane, namely *membrane testacea*, is also characterized by two layers. (C) SEM image of the cuticle on the surface of the *Gallus* eggshell, showing a patchy and cracking pattern. (D) SEM image of the radial section of the *Gallus* eggshell. The white arrow indicates the cuticle layer that lies on the calcitic eggshell. (E) Raman chemical image with peak targeting at 967 cm^{-1} which is attributed to HAp. The yellow area represents the patchy distribution of the inner HAp cuticle layer on the *Gallus* eggshell. The calcitic eggshell that is not covered by the inner HAp cuticle layer is shown in the brown area. The dotted circle corresponds to the spectrum shown in (F). (F) Spectrum collected in the dotted-circle area of the Raman chemical image shown in (E). Two significant peaks at 967 cm^{-1} and 1087 cm^{-1} represent HAp and calcite, respectively.

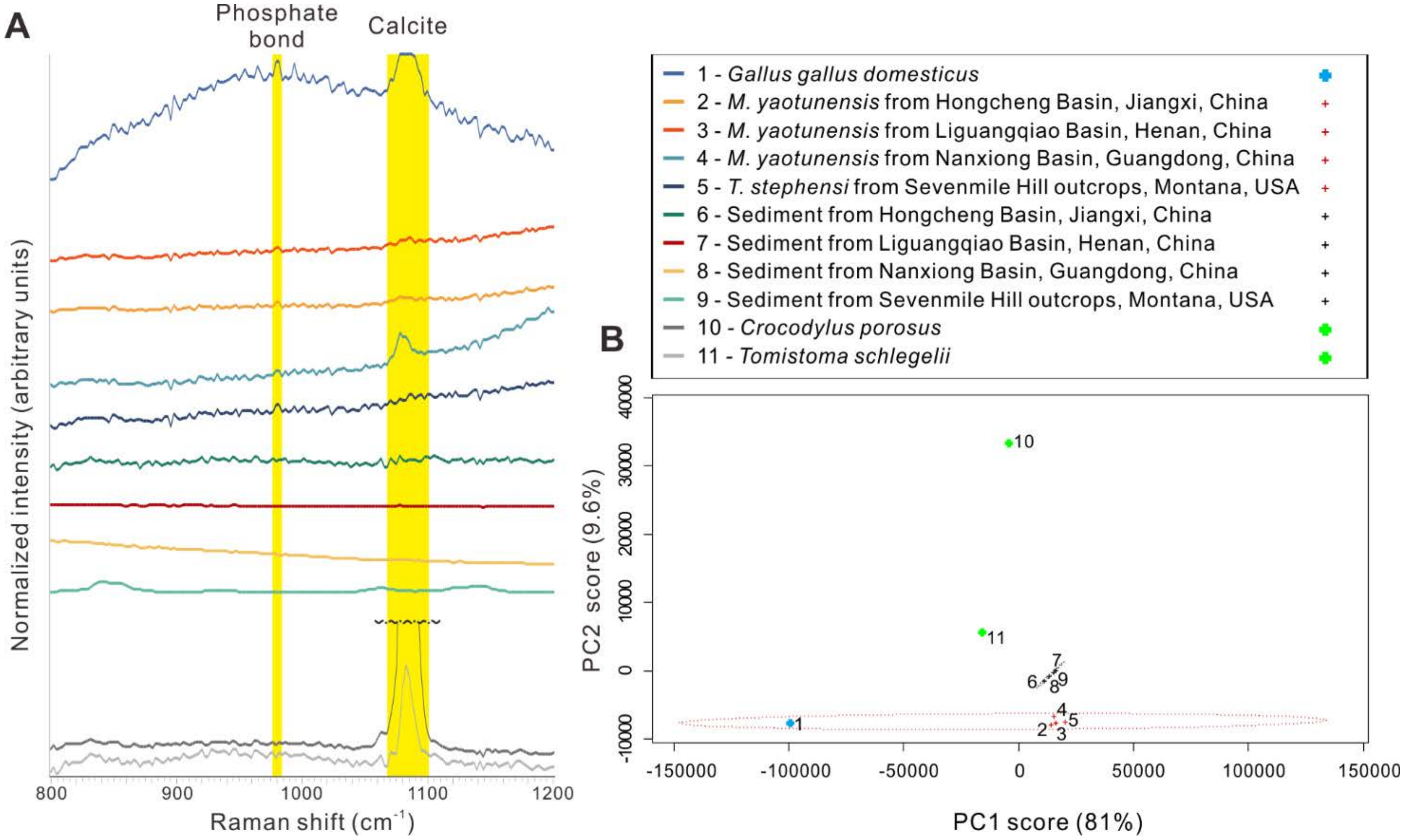


Figure 3-2 Raman spectra and chemometric analysis. (A) Raman spectra derived from chicken, crocodilian, fossil dinosaur eggshells, and surrounding sediments. The peaks around 972-986 cm-1 and 1063-1097 cm-1 are marked by yellow bars, indicating the calcite and phosphate bonds. (B) The principle component chemometric analysis on the spectral area of 800-1200 cm-1 shown in (A) demonstrates significant disparities between dinosaur/chicken eggshells, crocodilian eggshells, and sediments.

3-3 Results

The cuticle layer on the *Gallus* eggshell was easily observed with the naked eye. The RI Raman spectrum from the *Gallus* eggshell shows a significant peak at 1087 cm^{-1} that arises from the calcite, which is the major component of eggshell (Figure 3-1F). Another intense peak at 967 cm^{-1} was assigned to the $v_3PO_4^{3-}$ symmetric stretching vibrations (Walters et al., 1990; Gergely et al., 2010; Frost et al., 2014; Igic et al., 2015). Targeting the 967 cm^{-1} peak, the Raman surface scan shows the patchy distribution of the HAp layer overlying the calcitic eggshell (Figure 3-1E). The result demonstrates detectability of the inner HAp layer of the cuticle by RS.

On the outside of *Macroolithus yaotunensis* and *Triprismatoolithus stephensi* eggshell fragments, we also found peaks in these spectral regions (Figure 3-2A & Appendix I (electric version only)). RII showed two intense broad peaks that are located between 1063-1097 cm^{-1} and 972-986 cm^{-1} in the spectra. The spectral range of 1063-1097 cm^{-1} can be assigned to the C-O bond of calcite, which is observable in the spectra from all eggshells. The 972-986 cm^{-1} spectral ranges arose possibly from the phosphate (PO_4^{3-}) or hydrogen phosphate (HPO_4^{2-}) (Sauer et al., 1994; Crane et al., 2006; Igic et al., 2015). Importantly, the 972-986 cm^{-1} spectral ranges are present in the spectra from the chicken and dinosaur eggshells but absent in the ones from the crocodilian eggshells and surrounding sediments. The chemometric analysis using ChemoSpec suggests that both chicken and dinosaur eggshells show similar spectral pattern between 800 cm^{-1} and 1200 cm^{-1} (Figure 3-2B & Appendix I (electric version only)). In addition, the spectra from the crocodilian eggshells and surrounding sediments occupy different chemospaces from the ones of dinosaur and chicken eggshells (Figure 3-2B & Appendix I (electric version only)).

Under the polarizing microscope, the *Macroolithus* eggshell from the Hongcheng Basin of Jiangxi, China, displayed distinct two crystalline layers overlain by an enigmatic layer and surrounding sediment (Figure 3-3A). These features are also present in the other two *Macroolithus* eggshells. The uneven thickness of the prismatic layer in the Jiangxi *Macroolithus* eggshells was a result of unpolished natural fracture surface of the section (Figure 3-3B). A possible patchy and flake-like cuticle layer was observed on the outer surface of the *Macroolithus* and *Triprismatoolithus* eggshells (Figure 3-3C & Figure 3-4B). Furthermore, an enigmatic protruding fiber-like structure was recognized in the

Triprismatoolithus eggshell (Figure 3-4C-D). The diameter of the fiber-like structure is approximately 3 μm.

We performed ten elemental line-mappings on each eggshell with EPMA and targeted phosphorus of the HAp. Of the total 30 line mappings on the three *Macroolithus yaotunensis* eggshell, only two of them, which were from the Jiangxi and Guangdong specimens, show a significant phosphorus peak on the boundary between the eggshell and surrounding sediment (Figs. 3D & 3F). The elemental analysis also indicates the scarcity of the phosphorus in the surrounding sediment. In addition, the P concentration increases from the mammillary layer to the prismatic layer in all analyzed oviraptorid eggshells (Figure 3-3D-F & Appendix II (electric version only)).

In the EPMA line-scan on the *Triprismatoolithus stephensi* eggshell, three significant peaks for P were observed (Figure 3-4E). The peak on the boundary between the eggshell and surrounding sediment indicates possible cuticle preservation (Figure 3-4E). However, the other two peaks were seen in the sediment and on the boundary between the external layer and prismatic layer. The variation of P concentration between different eggshell layers was also observed in *Triprismatoolithus stephensi* eggshell (Figure 3-4E & Appendix II (electric version only)). Although the P concentration within the mammillary and prismatic layers shows little variation, the external layer has a significantly lower concentration of P than the mammillary and prismatic layers (Figure 3-4E & Appendix II (electric version only)).

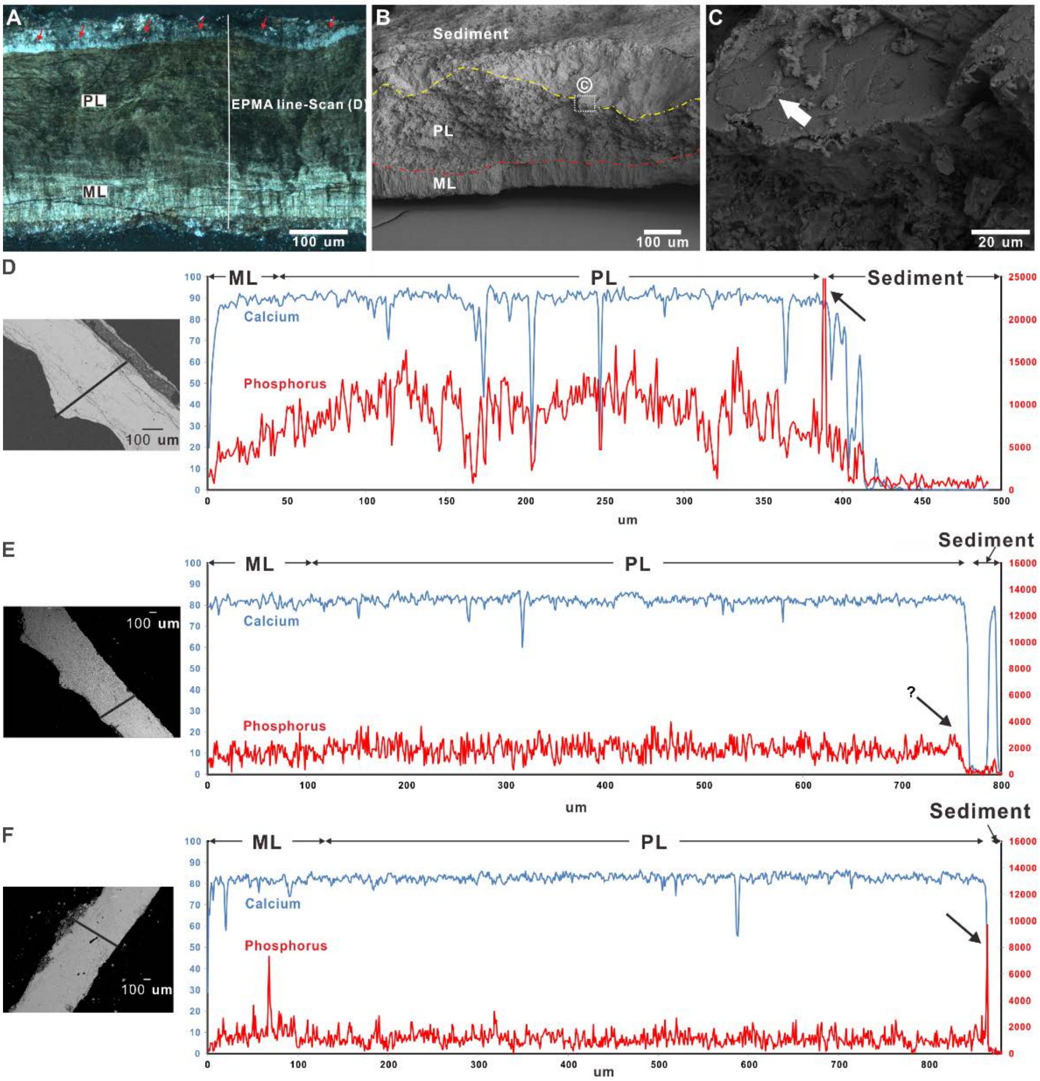


Figure 3-3 Microscopic images of *Macroolithus yaotunensis* eggshell from Henan, Jiangxi, and Guangdong and their line-scan spectra. (A) The *Macroolithus yaotunensis* eggshell (NMNS CYN-2004-DINO-05-I) from Jiangxi under the polarized light microscope. The red arrows indicate the indistinct boundary between the sediment and an enigmatic layer. This enigmatic layer probably was formed by the interaction between organics of the egg and surrounding sediment. The location of the EPMA line-scan spectra in (D) is indicated by the white solid line. In this eggshell image, a smooth boundary between the prismatic and mammillary layers (PL and ML, seen as dark and light zones) is clearly observed. (B) SEM image of radial untreated fracture of the *Macroolithus yaotunensis* eggshell. The boundary between the sediment and prismatic layer is marked by yellow dashed line based on their distinct structural features. The boundary between ML and PL is marked by the red dashed line. The ML shows the distinct vertical mammillae structure. (C) Close-up image of the area in white box in (B). Possible preservation of cuticle is indicated by the white arrow, showing patchy and flaky structures similar to the cuticle on the modern chicken eggshell (Figs. 1C & 1D). (D)-(F) The microscopic image to the left of the spectra shows the radial cut section of studied *Macroolithus yaotunensis* eggshells seen in the SEM coupled

with the EPMA and elemental line-scan track marked as black lines. (D) The spectra illustrate the distribution of Ca and P across the eggshell from the Hongcheng Basin in Jiangxi shown in (A), from innermost (left) to outermost, as indicated by the white line in the microscopic image. The Ca spectrum clearly marks the extent of the calcitic eggshell. A significant peak that is marked by a black arrow demonstrates a relatively high concentration of P, indicating the possible preservation of the cuticular HAp layer. (E) The spectra illustrate the distribution of Ca and P across the eggshell from the Liguangqiao Basin in Henan, from innermost (left) to outermost. The Ca spectrum clearly marks the extent of the calcitic eggshell. A slightly higher amount of P near the interface between the eggshell and sediments, as indicated by a black arrow, is observed. (F) The spectra illustrate the distribution of Ca and P across the eggshell from the Nanxiong Basin in Guangdong, from innermost (left) to outermost. A significant peak that is marked by a black arrow demonstrates a relatively high concentration of P, indicating the possible preservation of the cuticular HAp layer. ML, mammillary layer; PL, prismatic layer.

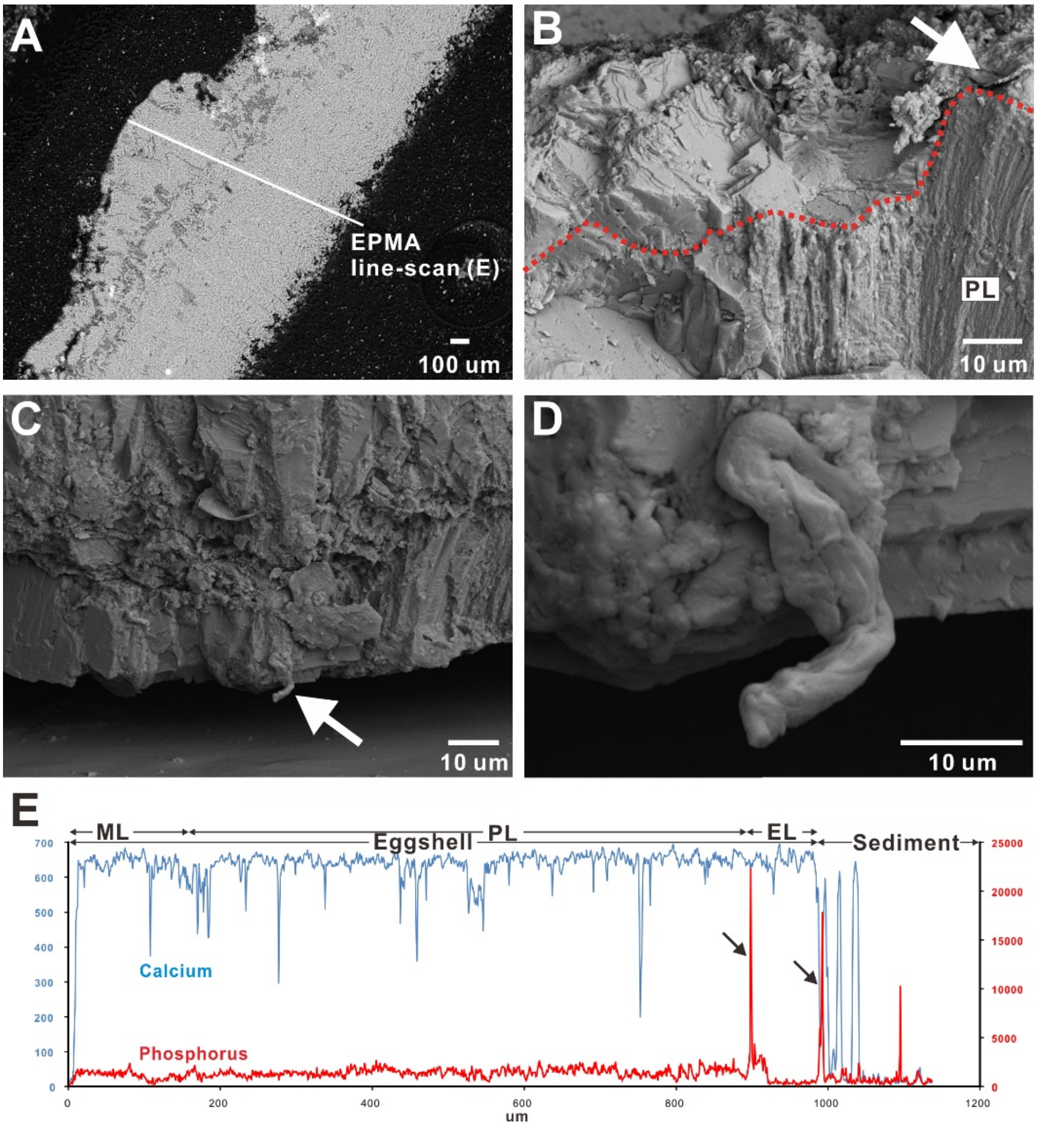


Figure 3-4 SEM images of the *Triprismatoolithus* eggshell and EPMA line-scan spectra. (A) The radial cut section of studied *Triprismatoolithus* eggshell in the SEM coupled with the EPMA. (B) The probable flake-like cuticle structure atop the eggshell, marked by the white arrow. The red dotted line marks the outermost boundary of the prismatic layer. (C) An enigmatic structure (white arrow) protruding from the mammillary layer, possibly a fiber of the *membrana testacea* extending into the mammillary layer. (D) Enlargement of the possible fiber. (E) Line scans across eggshell in (A). The scan shows a high concentration of P at the boundary between the eggshell and surrounding sediment. Two other peaks of P were observed on the boundary between the external and prismatic layer and in the sediment. The P concentration does not differ between the mammillary and prismatic layers; however, the external layer showed a significantly lower concentration of P than the mammillary and prismatic layers. EL, external layer; ML, mammillary layer; PL, prismatic layer.

3-4 Discussion

3-4-1 Elemental Analysis of Theropod Eggshells

While previous studies have reported possible preservation of cuticle and *membrane testacea* (Chow, 1954; Kohring & Hirsch, 1996; Grellet-Tinner, 2005; Jackson & Varricchio, 2010; Reisz et al., 2013; Yang et al., 2015), none of these studies employed chemical analyses to test this hypothesis. In this study, elemental analysis suggests the preservation of the inner hydroxyapatitic cuticle layer based on the high concentration of P at the boundary between eggshell and sediment. However, the peak that corresponds to a high concentration of P is not always present in each elemental line-scan. For instance, on the *M. yaotunensis* eggshell sample from the Liguangqiao Basin (Figure 3-3E), a probable P-rich zone, instead of an abrupt peak, is shown near the boundary between the eggshell and surrounding sediment. RS analysis indeed revealed the existence of phosphates. Since RS scans a larger area than EPMA does, we suggest that the absence of an abrupt peak for a P-rich zone in those 28 line-scans is a result of incomplete preservation of the cuticle layer or a sampling bias during the EPMA analyses. The elemental analysis also shows that P is rare in the surrounding sediment from both the Nanxiong Group of China and the Two Medicine Formation of Montana, United States. The deficiency of P in the sediment thus argues against an allochthonous origin of the P in the outermost part of the eggshell (Figs. 3D-F & 4E). The chemometric comparison of the spectra derived from sediments also suggests the depletion of phosphate minerals in the sediments. Therefore, the peak in the sediment surrounding the *Triprismatoolithus stephensi* eggshell might be derived from the eggshell specimen itself.

The enigmatic fiber-like structure near the base of the mammillary layer in the *Triprismatoolithus* eggshell (Figure 3-4D) may be a capillary vessel of the chorioallantoic membrane or a fiber of the *membrana testacea*. The elemental analyses cannot provide evidence for the preservation of the capillary vessels of the chorioallantoic membrane. SEM images show that the vessels in the chorioallantoic membrane of modern chicken eggshells range in size from 3 to 10 µm (Maibier et al., 2016), similar to the fiber-like structure we observed in the *Triprismatoolithus* eggshell (Figure 3-4D). However, the fiber-like structure in the *Triprismatoolithus* eggshell does not appear to be hollow, unlike a blood vessel (Schweitzer et al., 2005a). It is therefore possible that the enigmatic fiber-like structure in the *Triprismatoolithus* eggshell represents a part of fossilized *membrana testacea*, which has never been described in theropod dinosaurs. The *membrana testacea* fibers in a chicken egg occasionally penetrate through the mammillary base (Ahmed, Suso & Hincke, 2017) and are of the same size of around 3 μm as the fiber-like structure we observed in the *Triprismatoolithus* egg (Figure 3-4D). However, the hypothesis of fossilized *membrana testacea* requires more supporting evidence.

3-4-2 Variation of P Concentration in Eggshells

Despite numerous studies on element distribution in modern avian and reptilian eggshells, dinosaur eggshells were rarely investigated from a chemical perspective. Several studies posited that P is a critical element that regulates eggshell growth (Fink et al., 1993; Dennis et al., 1996; Fraser, Bain & Solomon, 1999; Cusack, Fraser & Stachel, 2003). In *Gallus gallus domesticus* eggshells, a pattern of increasing P concentration from the mammillary layer to the prismatic layer has been reported (Cusack, Fraser & Stachel, 2003). This pattern is similar to what we observed in oviraptorid eggshells (Figure 3-3D-F). The deficiency of P in the surrounding sediments demonstrates that the distribution pattern of P in the studied eggshells is endogenous. Since ornithological research had suggested that P is an inhibitor of calcite growth during eggshell formation (Fink et al., 1993; Dennis et al., 1996; Fraser, Bain & Solomon, 1999; Cusack, Fraser & Stachel, 2003), the similarity of P distribution between oviraptorid dinosaur and modern avian eggshells suggests that the oviraptorid dinosaurs studied by us already possessed a similar eggshell formation mechanism to that of extant birds.

Moreover, Cusack, Fraser & Stachel (2003) also observed that the P concentration increases more sharply between the mammillary and prismatic layers in the eggshell of younger birds than in those of older birds. Therefore, the difference in P distribution between young and older birds can probably help paleontologists decipher whether an oviraptorid clutch was laid by a single female or by several females. If the whole clutch was produced by a single female or by several females of a similar age, all eggs should exhibit a similar pattern of P concentration increase from the mammillary layer to the prismatic layer. Conversely, different patterns of increase would suggest that females of different ages contributed to a single clutch. Varricchio et al. (2008) compared the ratio of clutch mass to adult mass and proposed that an oviraptorid clutch was produced by several females. Yang et al. (2016) have provided preliminary supportive results based on statistical analyses of eggshell P distribution and external morphology in the same oviraptorid clutch.

On the other hand, in the *Triprismatoolithus stephensi* eggshell, P concentration varies slightly between the mammillary and prismatic layer but decreases significantly from the prismatic layer to the external layer (Figure 3-4E). Such a pattern of P distribution differs from the one in oviraptorid or modern bird eggshells we discussed previously. Moreover, unlike a single peak of high P concentration in oviraptorid and modern eggshells, three distinctive peaks of high P concentration are present in the *Triprismatoolithus stephensi* eggshell. Based on the general deficiency of P in the surrounding sediment, we posit that the P peak in the sediment surrounding the *Triprismatoolithus stephensi* eggshell is a result of a detached cuticle layer. The peak at the boundary between the external layer and surrounding sediment represent the putative cuticle layer (Figure 3-4E). However, the peak at the boundary between the prismatic and external layers was not reported previously in any avian eggshells (Figure 3-4E). If the sequestration of P is a crucial factor in the termination of calcite growth, the high concentration of P on the boundary between the prismatic and external layers represents a possible temporal hiatus between the prismatic and external layers in the *Triprismatoolithus* eggshell.

3-4-3 Interpretation of Raman Spectra

In the Raman study of the fossil eggshells, the peak at 967 cm^{-1} of *Gallus* eggshell was not seen in all spectra, but a broad peak ranging from 972-986 cm^{-1} was detected instead (Figure 2A). The broad peak ranging from 972-986 cm^{-1} represent the phosphate groups, as indicated in (Igic et al., 2015). Three hypotheses can be formulated to explain the different spectral patterns from 960 cm^{-1} to 980 cm^{-1} in extant cuticle vs. the fossil eggshells.

First, theropod dinosaurs might have used whitlockite, a phosphate mineral containing hydrogen phosphate anions (HPO_4^{2-}), to form the inner cuticle layer instead of HAp. Whitlockite is the second most abundant mineral in biological calcified tissues, accounting for around 20% of bone mineral (Driessens & Verbeeck, 1990; Jang et al., 2014; Jang et al., 2015). It is also possible that the HAp of the inner cuticle layer is in non-stochiometric form, and hence part of the phosphate anions is occupied by hydrogen phosphate (HPO_4^{2-}) (Rey et al., 2011; de la Pierre et al., 2014).

Second, the original HAp of the inner cuticle layer could have been transformed to whitlockite. Jang et al. (2014) showed that HAp transforms into dicalcium phosphate dihydrate (DCPD, $CaHPO_4 \cdot 2H_2O$) at 70 °C. The DCPD is then converted into whitlockite ($Ca_9(MgFe)(PO_4)_6PO_3OH$) by incorporating Mg^{2+} or Fe^{2+} when the pH decreases. In natural environments, such as the Nanxiong Formation and Two Medicine Formation, burial and diagenetic temperatures over 70 °C are unlikely except by an intrusion of igneous origin. However, geological investigations did not provide any evidence for such igneous intrusions in the Nanxiong Basin (Erben, 1995). At the Sevenmile Hill outcrops in Montana, United States, Foreman et al. (2008) reported an altered volcanic ash layer (bentonite) that is depleted in P. However, the volcanic ash layer was deposited prior to the eggshells (Jackson & Varricchio, 2010).

Third, the P we detected might be derived from the surrounding sediments during diagenesis. This is inconsistent with the preservation of pigments in the Nanxiong Basin eggshells and absence of igneous intrusions in both localities which suggests that the eggshells we studied experienced very little diagenesis (Erben, 1995; Foreman et al., 2008; Wiemann et al., 2017).

3-4-4 Pigmentation on Theropod Eggshells

As noted above, the discovery of protoporphyrin in oviraptorid dinosaur eggshells from all three localities where the eggshells for this study were collected (Table 1; Wiemann et al., 2017) is consistent with the cuticle preservation. Although Wilson et al. (2017) indicated that pigment deposition and cuticle formation are not codependent, the preserved protoporphyrin was probably from the cuticle layer. Thomas et al. (2015) performed Raman spectroscopy and mass spectrometry to show the detectability of pigments in extant avian eggshells. Our Raman analyses also demonstrate detectability of pigments in fossil eggshells; however, the peaks in the spectra do not completely correspondent with the ones shown in Thomas et al. (2015), suggesting further Raman studies using mass spectrometry on dinosaur eggshells.

3-4-5 Nesting Ecology of Oviraptorid Dinosaurs

As noted, two nesting modes are recognized in birds, open and buried nesting (Varricchio & Jackson, 2016). Most birds build open nests either on the tree or on the ground (ostriches or emus), while the megapode birds bury their eggs in a mound. Therefore, all open nesting birds have eggshells of low porosity (Tanaka, Zelenitsky & Therrien, 2015). However, an intermediate mode, semi-open nests in oviraptorid dinosaurs, was recently proposed based on detection of pigments and porosity evaluation (Yang et al., 2015; Wiemann et al., 2017). Pigmented eggshells strongly suggest an open nesting mode. However, the porosity evaluation revealed a heterogeneous distribution of porosity—highest porosity in the lower middle part (buried) and lowest porosity in the blunt end (open) (Yang et al., 2015; Wiemann et al., 2017), thus indicating a semi-open nesting mode. This intermediate mode is consistent with the fluvial environment inferred by sedimentological investigations in the Nanxiong Basin (Erben, 1995). In such a humid fluvial environment, the risk of microbial invasions was much higher. The cuticular nanospheres, which are associated with humid environments and protect extant eggs from microbial invasions, were very likely present in the oviraptorid and alvarezsaurid dinosaur eggs from these fossil humid environments as well. Although we did not detect cuticular nanospheres in the dinosaur eggshell, our detection of a cuticle layer suggests it to have been an adaptation for the oviraptorid and alvarezsaurid dinosaurs nesting in a humid fluvial environment (D'Alba et al., 2016).

On the other hand, it was inferred that Mongolian oviraptorid clutches were deposited in a xeric environment. The evidence is the eolian nature (sand dune deposits) in the Baruungoyot and the Djadokhta formations (Norell et al., 1995). Although no Mongolian oviraptorid eggshells were included in our study, it appears likely that Mongolian oviraptorid eggs were also cuticle-coated for the prevention of water loss as in Adélie penguin eggs (Thompson & Goldie, 1990). Fanti, Currie & Badamgarav (2012) documented clutches of the oviraptorid *Nemegtomaia* from both the Nemegt and Baruungoyot formations that represent mesic and xeric habitats, respectively. Moreover, they also provided evidence for the lateral coexistence of mesic and xeric habitats in the Baruungoyot Formation and posited that *Nemegtomaia* and other Mongolian oviraptorid dinosaurs, nested near permanent or seasonal streams. In such a variable environment, the cuticle-coated eggs, therefore, would have been an adaptive trait that enhanced reproductive success of oviraptorid dinosaurs.

While it is uncertain that the alvarezsaurid eggshells were pigmented without further chemical studies, it is possible that alvarezsaurid dinosaur exploited similar nesting strategies as oviraptorid dinosaurs did.

3-4-6 Taphonomic Implications for Cuticle Preservation

The cuticle layer is a labile, easily lost structure that appears unlikely to be preserved during the fossilization process. Our study thus raises an important taphonomic question, i.e., how did the cuticle layer get preserved? Since the cuticle preservation observed by us appears to pertain to eggshell from clutches and not from dispersed eggshell, cuticle preservation probably is facilitated by fossilization of eggs in clutches. Furthermore, a layer of secondary diagenetic calcite is commonly observed on eggshells from fluvial deposits (Figure 3-3A; Jackson & Varricchio, 2010). This layer of secondary calcite may have been a rigid shield that protected the cuticle layer from mechanical removal.

Therefore, we hypothesize that the *in situ* preservation and the coverage of secondary calcite possibly protect the cuticle layer from being washed away or removed. More detailed microscopic observation of the association between the cuticle, secondary calcite layers, and surrounding sediment will possibly elucidate the taphonomic processes.

3-5 Conclusion

Our study suggests preservation of the inner cuticle layer in *Macroolithus yaotunensis* and *Triprismatoolithus stephensi* eggs based on elemental analysis and RS. The cuticle layer and semi-open nesting mode in humid environments may be key adaptations to protect the eggs from microbial invasions in a humid environment such as a fluvial plain, as does the cuticle layer of extant birds nesting in humid environments. In combination with the previous discovery of pigments in oviraptorid dinosaur eggshells, this study provides further evidence for preservation of fossilized soft tissues in the fluvial deposits, especially in the Cretaceous red bed basins of China. Further chemical studies on dinosaur eggshells will shed additional light on the reproductive biology of dinosaurs, as well as on taphonomic questions.

Chapter 4 Dinosaur Origin of Egg Color: Oviraptors Laid Blue-Green Eggs

PUBLICATION

Wiemann J, **Yang T-R**, Sander PN, Schneider M, Engeser M, Kath-Schorr S, Müller CE, and Sander PM. 2017. Dinosaur origin of egg color: oviraptors laid blue-green eggs. PeerJ 5:e3706. DOI: 10.7717/peerj.3706 (with some modifications)

ABSTRACT

Protoporphyrin (PP) and biliverdin (BV) give rise to the enormous diversity in avian egg coloration. Egg color serves several ecological purposes, including post-mating signaling and camouflage. Egg camouflage represents a major character of open-nesting birds which accomplish protection of their unhatched offspring against visually oriented predators by cryptic egg coloration. Cryptic coloration evolved to match the predominant shades of color found in the nesting environment. Such a selection pressure for the evolution of colored or cryptic eggs should be present in all open nesting birds and relatives. Many birds are open-nesting, but protect their eggs by continuous brooding, and thus exhibit no or minimal eggshell pigmentation. Their closest extant relatives, crocodiles, protect their eggs by burial and have unpigmented eggs. This phylogenetic pattern led to the assumption that colored eggs evolved within crown birds. The mosaic evolution of supposedly avian traits in non-avian theropod dinosaurs, however, such as the supposed evolution of partially open nesting behavior in oviraptorids, argues against this long-established theory. Using a double-checking liquid chromatography ESI-Q-TOF mass spectrometry routine, we traced the origin of colored eggs to their non-avian dinosaur ancestors by providing the first record of the avian eggshell pigments protoporphyrin and biliverdin in the eggshells of Late Cretaceous oviraptorid dinosaurs. The eggshell parataxon *Macroolithus yaotunensis* can be assigned to the oviraptor *Heyuannia huangi* based on exceptionally

preserved, late developmental stage embryo remains. The analyzed eggshells are from three Late Cretaceous fluvial deposits ranging from eastern to southernmost China. Reevaluation of these taphonomic settings, and a consideration of patterns in the porosity of completely preserved eggs support an at least partially open nesting behavior for oviraptorosaurs. Such a nest arrangement corresponds with our reconstruction of blue-green eggs for oviraptors. According to the sexual signaling hypothesis, the reconstructed blue-green eggs support the origin of previously hypothesized avian paternal care in oviraptorid dinosaurs. Preserved dinosaur egg color not only pushes the current limits of the vertebrate molecular and associated soft tissue fossil record, but also provides a perspective on the potential application of this unexplored paleontological resource.

Chapter 4: Oviraptor Egg Coloration

4-1 Introduction

Birds offer the most diverse displays of color and shape among modern vertebrates (Stoddard & Prum, 2011). In contrast to their closest modern relatives, the crocodiles, avian eggs range widely in size and shape, and the avian key innovation seems to be variation in color (Cassey et al., 2012). Nature's repertoire ranges from immaculate (homogeneously colored) reddish brown and white eggs in chicken (*Gallus domesticus*), to light beige with dark brown maculation (speckling) in the oystercatcher (*Haematopus ostralegus*), to light blue in the American robin (*Turdus migratorius*), to the intensive bluish-green of emu eggs (*Dromaius novaehollandia*e) at the end of the spectrum (Cassey et al., 2012).

All other amniotes, including non-avian reptiles and monotreme mammals, lack eggshell color (Packard & Seymour, 1997). Non-avian amniotes can protect their eggs by burying them (Leighton, Horrocks & Kramer, 2009), or by continuously guarding the nest (Komdeur & Kats, 1999). Colored eggs are present in most modern birds which build open nests, as the eggs are vulnerable due to periods without parental guarding (Komdeur & Kats, 1999; Gillis et al., 2012). Birds with biparental brooding behavior minimize the periods during which a clutch is unattended and vulnerable, and sometimes reduce egg coloration (Komdeur & Kats, 1999). Complete reduction of eggshell coloration is observed in many cavity nesting and cave-breeding birds (Hewitson, 1846) confirming the visual signaling component of egg color function (Castilla et al., 2007). Visual signaling resulting in camouflage of an egg clutch is largely dependent on eggshell coloration relative to the color shade of the nesting background (Wallace, 2007; Stoddard et al., 2016). Such negative signaling also offers protection against brood parasitism because of, e.g., elaborate egg color innovations that allow recognition of parasite eggs among the clutch (Newton & Gadow, 1896). In addition to signaling, numerous other functions of egg color pigments have been proposed, such as antimicrobial effects (Ishikawa et al. 2010), protection from solar radiation (Lahti, 2008), and eggshell mechanical reinforcement (Gosler, Higham & Reynolds, 2005). In a phylogenetic analysis of egg shell coloration and color patterning, Kilner (2006) concluded that the ancestral egg color of avian of extant birds was white, and that egg coloration evolved multiple times within crown birds 46(see Kilner, 2006).

This phylogenetic inference ignores the fact that many birds with white eggs, including ostrich (*Struthio*), rhea (*Rhea*) and elephant bird (*Aepyornis*) contain minor amounts of eggshell pigment, and that their reduced pigment most likely represents an evolutionary reaction to the brooding-based reduced selection pressure on coloring their eggs (Kennedy & Vevers, 1976).

We hypothesize egg coloration evolved after the switch from burying eggs to building an open and exposed nest (consistent with Gillis et al., 2012). Selection for egg color would only have occurred after the eggs themselves became visible to parents, conspecifics, predators, or parasites (Kilner, 2006).

While most dinosaurs buried their eggs (reviewed by Varricchio & Jackson, 2016), there is ample evidence that bird-like, non-avian eumaniraptoran dinosaurs, i.e., Oviraptorosauria, Dromaeosauridae, and Troodontidae, built open ground nests with at least partially exposed eggs (Norell et al., 1995; Varricchio & Jackson, 2016). Partial exposure accounts for the arrangement of their strongly elongated eggs stacked and partially buried almost vertically in the nest material in circular layers either with (seemingly primitive) or without (derived) an empty space in the center of the nest (Norell et al., 1995). Late Cretaceous oviraptorosaurian eggs from China and Mongolia (Norell et al., 1995; reviewed in Varricchio & Jackson, 2016) are frequently preserved, and because they are laid in exposed, partially open nests (Norell et al., 1995), they may have been pigmented like many bird eggs. Only two chemical compounds act as avian eggshell pigments and give rise to virtually all observed bird egg colors and patterns–the tetrapyrrols protoporphyrin (PP) and biliverdin (BV) (Kennedy & Vevers, 1976). Both are participants in the vertebrate heme cycle: protoporphyrin is a reddish-brown heme precursor, while biliverdin is a blue–greenish heme catabolite (Ryter & Tyrrell, 2000). In contrast to the linear BV, the cyclic PP exhibits a stronger resonance stabilization (Falk, 1964). Due to their different metabolic functions, PP and BV have distinctively different chemical properties: while PP is lipophilic and rather unreactive, BV is much more reactive due to its hydrophilic, oxidated, linear arrangement (Gorchein, Lim & Cassey, 2009). BV is distributed throughout the entire thickness of the prismatic layer in eggshells, most probably linked to matrix proteins, while PP is currently thought to be present in high concentrations only in the outermost eggshell cuticle layer (Wang et al., 2009). Related avian pigments are incorporated into integumentary structures, such as, for example, the PP relative uroporphyrin III which occurs as red turacine pigment in the feathers of herbivorous, musophagid birds (Rimington, 1939). Structurally, the two avian eggshell pigments show a similarity to the most common vertebrate pigments eu- and pheomelanin, in being N-heterocycles (Watt, Bothma & Meredith, 2009) although their origins are very different in vertebrate secondary metabolism (Kubo & Furusawa, 1991).

In terms of pigment taphonomy, the oldest confirmed record of eggshell PP and BV traces is in subfossil moa eggs from New Zealand (Igic et al., 2010) which demonstrates their preservation potential on a time scale of 103 years, but also the loss of the more labile BV through time due to degradation processes, dissolution and transport via percolating aqueous fluids. Other related biomolecules with a reported fossil record are hemes (Greenwalt et al., 2013), and chlorophylls (Leavitt, 1993). Both have been identified with minimal or no diagenetic alteration from Mesozoic and Cenozoic fossil deposits, supporting the possibility of eggshell pigment preservation in fluvial or alluvial oxidative deposits such as those from eastern and southern China. We identified unmodified, preserved PP and BV eggshell pigments in all three oviraptorid samples and proved that these eggshells were the sole source of pigments by demonstrating the absence of BV and PP in the investigated sample of adjacent sediment. We also provide support for the preservation of dinosaur eggshell cuticle (previously suggested by Mikhailov, Bray & Hirsch, 1996; Schweitzer et al., 2002; Varricchio & Jackson, 2004) based on cuticular PP storage. These observations phylogenetically extend the presence of an avian-like eggshell pigmentation back to oviraptorids. Using the known concentrations of our commercial pigment standards and PP and BV concentrations in emu eggshell as a sensitivity control and quality marker for our analytic system, we reconstructed a visually evident blue–green egg color for *Heyuannia* incorporating experimental and taphonomic corrections. Our eggshell zonal porosity reevaluation reconstructed an at least partially open nest for the oviraptorid *Heyuannia huangi* (based on Deeming, 2006; Varricchio et al., 2013; see section 4-2-6).

4-2 Material and Methods

4-2-1 Extant Eggshell Material

The emu eggshells (*Dromaius novaehollandiae*) were produced by captive birds and are stored in the ZFMK collections (ZFMK uncat.). Emu eggshell is reported to contain minimal amounts of PP in addition to some of the highest naturally occurring amounts of BV (Gorchein, Lim & Cassey, 2009).

4-2-2 Fossil Eggshell Material

Elongatoolithidae (Zhao, 1975)
Macroolithus (Zhao, 1975)
    Macroolithus yaotunensis (Zhao, 1975)
    (Laid by the oviraptorid *Heyuannia huangi*)

We sampled three oviraptorid *Macroolithus yaotunensis* eggs from the collections of the NMNS and STIPB covering three geographically and taphonomically distinct Chinese deposits. Investigated specimens were collected in the Liguanqiao Basin near Nanyang in the province of Henan (STIPB E54/1), from the Hongcheng Basin in the province of Jiangxi (NMNS CYN-2004-DINO-05/I), and the Nanxiong Basin in province of Guangdong (STIPB E54/3). Detailed descriptions of the localities in context of geological and taphonomic settings are introduced below. Macroscopically, all oviraptorid eggshell samples had a blackish to blackish-brownish (after cleaning them from adherent sediment) color, revealing a very subtle shimmer of blue–green at angled light conditions.

Historically, samples derived from the Liguanqiao Basin are Late Cretaceous in age and derived from the fluvial/alluvial deposits (red sandstones) of the Hugang Formation. They have been housed in STIPB since 1983 and were previously described by Erben (1995). Preserved oviraptorid eggs from the Hongcheng Basin in the province of Jiangxi were obtained from the Late Cretaceous Tangbian Formation which comprises fluvial red sandstones. The Hongcheng Basin and the Nanxiong Basin may belong to the same extended basin complex (Liu, 1999). The Late Cretaceous strata of the Nanxiong Basin are divided into the Yuanpu Formation and the overlying Pingling Formation. The Yuanpu

Formation, which might be correlated with the fossil-rich Mongolian Djadochta Formation, yielded our eggshell samples from alluvial sediments (red silt-sandstones), and is dated as Maastrichtian in age (Zhao, 1991).

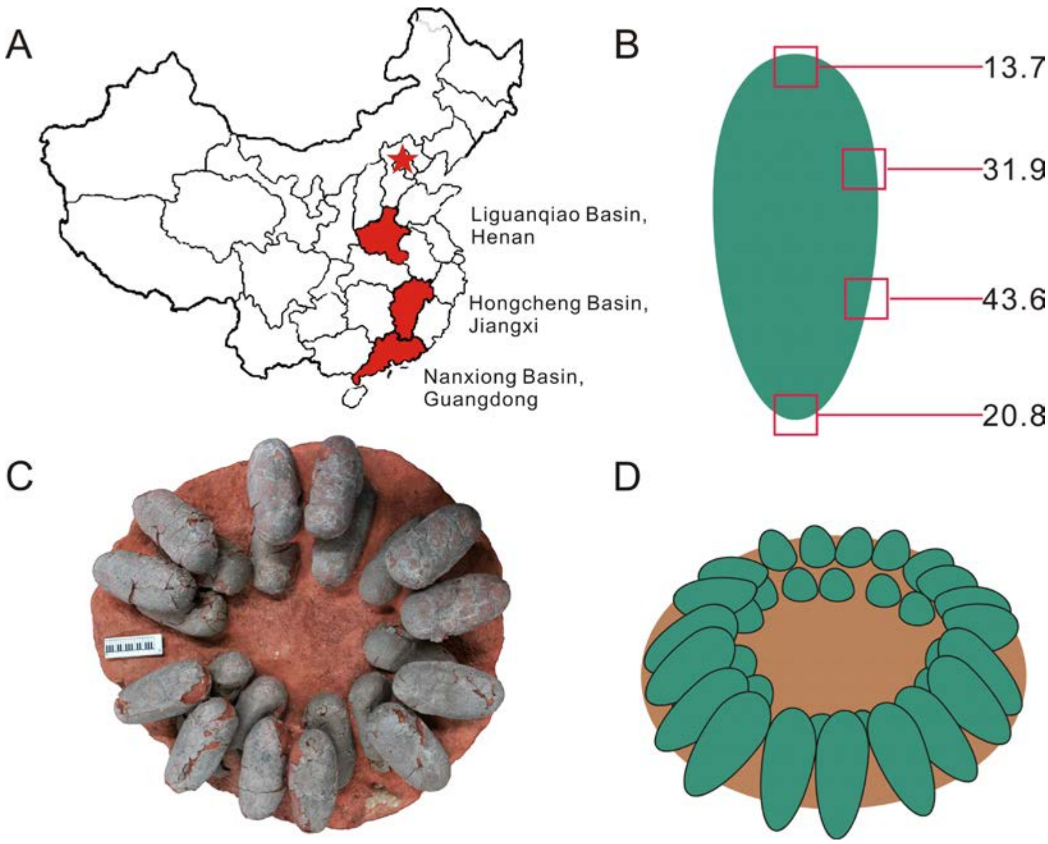


Figure 4-1 Provenance of *Heyuannia* eggshell, reconstructed zonal egg water vapor conductance, oviraptor clutch structure, and corrected, reconstructed egg color. (A) Geographical map of China. The capital city, Beijing, is indicated by the red star. Red shaded provinces indicate the three different localities where the specimens were collected: the Liguanqiao Basin in Henan, the Hongcheng Basin in Jiangxi, and the Nanxiong Basin in Guangdong. (B) The reconstructed color and average zonal water vapor conductance of the left Jiangxi *Heyuannia huangi* egg (NMNS CYN-2004-DINO- 05/I) calculated from BV and PP concentrations and porosity measurements (see Section 4-2-6). (C) Top view of an oviraptor clutch (PFMM 0010403018). This clutch illustrates how eggs are arranged in pairs with their blunt ends pointing to the clutch center. The eggs are arranged in layers separated by sediment. (D) Reconstruction of a partially open oviraptorid nest. Note that the original inclination of the eggs would have been steeper than their preserved attitude (C) due to sediment compaction.

One of two preserved complete eggs (Figure 4-1A) from the Chinese province of Jiangxi (NMNS CYN-2004-DINO-05) which were previously assigned to the oviraptorid egg parataxon *Macroolithus yaotunensis* was sampled over four zones of the egg (Figure 4-1B and Figure 4-2B), prepared for histology, and then used for porosity measurements (see section 4-2-6). These four zones represent the blunt, middle, and acute parts of the egg, and were separated to approach zonal differences in porosity values which were tested for maximum porosity at the mid portions to indicate egg storage in an open nest (based on Varricchio et al., 2013). Measured porosity values were compared to published dinosaur and avian porosity patterns and used to calculate the eggshell water vapor conductivity. Samples for chemical analyses were taken separately. Sediment adhering to the complete eggs (NMNS CYN-2004-DINO-05/I) was sampled additionally to confirm that we are not dealing with wholesale sample contamination. A single sediment sample (red silty sandstone) was available to test against wholesale contamination with BV and PP of the sample since only the complete oviraptorid eggs from the province of Jiangxi provided original, attached matrix sediment. The two-remaining fossil oviraptor eggshell samples represent isolated fragments freed of original matrix.

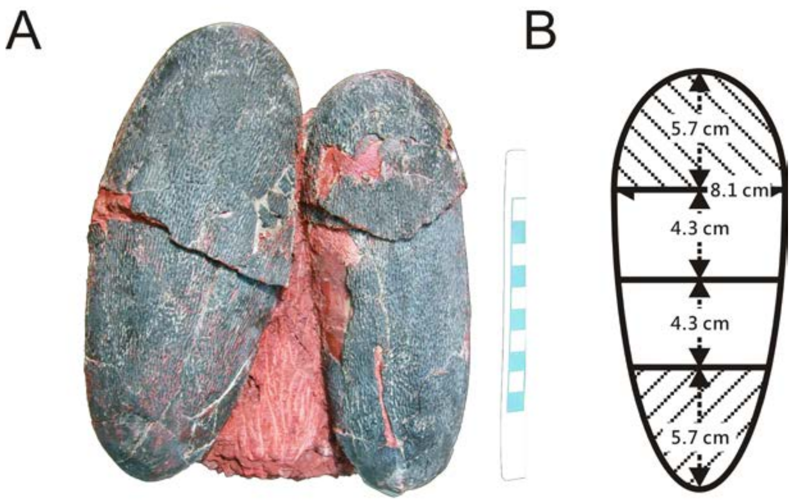


Figure 4-2 (A) Pair of oviraptorid *Heyuannia* eggs (NMNS CYN-2004-DINO-05) from the Chinese province of Jiangxi before sampling. Porosity measurements and calculations of water vapor conductance are based on these eggs. Pieces of eggshell from each of the four zones depicted in (B) were used in porosity measurements. (B) Egg model separated into four zones used for zonal porosity measurements. Therefore, double half-prolate spheroids and cone models of the idealized egg were used to estimate the zonal surface areas to eventually approximate water vapor conductance. Zone 1 represents the blunt end of the egg, zones 2 and 3 the mid portions, and zone 4 represents the pointed end of the egg.

4-2-3 Solvents and Equipment

In our analyses, we used protoporphyrin IXα and biliverdin hydrochloride as commercial standards and purchased these from Sigma Aldrich, UK. Disodium EDTA was obtained from Merck, Germany. Acetic acid (100%, LC-grade) and acetonitrile (LC-MS-grade) were also purchased from Merck, Germany, and from Sigma Aldrich, UK.

For extraction of the eggshell color pigments and filtration of the extract, we used 1.5 mL light-protecting polypropylene Eppendorf Amber microcentrifuge tubes and 0.5 mL standard conical Eppendorf microcentrifuge tubes. For vortex-mixing, we used a vortex mixer K neoLab (7-2020) and for centrifuging an Eppendorf centrifuge. Before injecting the eggshell extracts into the mass spectrometer, we filtered them by using a Chromafil O-45/3 PTFE disposable syringe filter holder (pore diameter: 0.45µm, filter diameter: 3 mm) on a 1.00 mL Injekt-F sterile syringe with a Sterican cannula on top.

Mass spectra were recorded on a micrOTOF-Q mass spectrometer (Bruker) with an ESI-source coupled with an HPLC Dionex Ultimate 3000 instrument (Thermo Scientific) using an EC50/2 Nucleodur C18 Gravity 3 µm column (Macherey-Nagel).

4-2-4 Extraction and pigment detection

The eggshell samples we used for pigment analysis were separately stored in air-tight plastic ziplets, which were protected from light in opaque paper boxes. We used eggshell fragments of at least 0.036 cm^2 surface area, weighing between 184 mg and 562 mg (Table 4-1). These eggshell fragments were cleaned from attached sediment with deionized, distilled water and then broken into smaller pieces.

The following extraction procedure is based on the method established by Gorchein, Lim & Cassey (2009).

Due to the greater polarity of BV as compared to PP, BV is partially dissolved in the aqueous EDTA solution; this results in a significant loss of BV during the extraction process. To quantify the amount of BV dissolved in the EDTA, the EDTA supernatants were stored for later UV/Vis measurements. The decalcification routine was repeated three times for BV and PP extraction.

Reverse-phase HPLC was run at a flow rate of 0.3 mL/min. HPLC was started with 90% H_2O containing 0.1% acetic acid. The gradient started after 1 min and reached 100% acetonitrile after 14 min. For an additional 7 min, the column was flushed with 100%

acetonitrile (containing 0.1% acetic acid). For the BV analysis, 15 μL sample solution were injected, and 20 μL for the PP detection.

Data were collected in positive full scan MS mode over the range of 50 – 1000 m/z, using a capillary voltage of 4.5 kV and an end plate offset of -500 V. The dry heater of the ESI source was set at 200°C. Nitrogen desolvation and nebulizer gas flow was 10.0 L/min, the nebulizer was run at 2.2 bar. Time-Of-Flight (TOF) detection allowed the determination of the accurate masses of BV and PP.

The observed elution order was as follows: BV (after 8 min; double peak indicates at least two isomers in acetonitrile-acetic acid) and PP (after 14 min; double peak indicates at least two isomers in acetonitrile-acetic acid).

Empirical relationships for estimating preserved BV concentration:

$$c_{BV}^{tot} \geq c_{BV} \times m_{X1g} \times f_{ex} \times f_c \qquad (4\text{-}1)$$

c_{BV}^{tot}=preserved total amount of BV stored into 1 g of eggshell $\left[\frac{\text{nmol}}{\text{1g(eggshell)}}\right]$

c_{BV}=ESI MS concentration approximation $\left[\frac{\text{nmol}}{\text{Xg (mass eggshell fragment)}}\right]$

m_{X1g}=mass multiplication factor for each eggshell fragment mass to reach 1g

f_{ex}=const. (for our extraction routine)≈3

f_c=const. (for empirical correction)≈4

$$\rightarrow 12 \times c_{BV} \times m_{X1g}$$

Empirical relationships for estimating preserved PP concentration:

$$c_{PP}^{tot} \geq c_{PP} \times m_{X1g} \times f_{ex} \times f_c \qquad (4\text{-}2)$$

c_{PP}^{tot}=preserved total amount of PP stored into 1 g of eggshell $\left[\frac{\text{nmol}}{\text{1g(eggshell)}}\right]$

$$c_{PP}=\text{ESI MS concentration approximation } \left[\frac{\text{nmol}}{\text{Xg(mass of each eggshell fragment)}}\right]$$

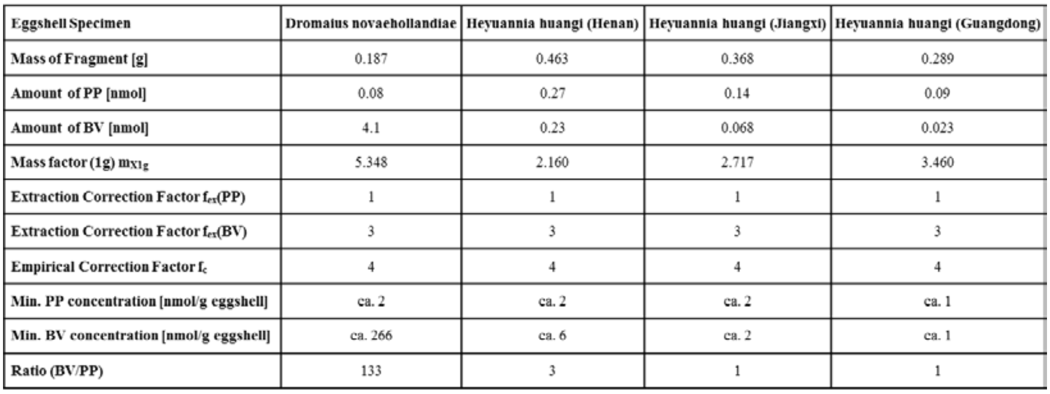
$$m_{X1g}=\text{multiplication factor for each eggshell fragment mass to reach 1g}$$

$$f_{ex}=\text{const. (for our extraction routine)}\approx 1$$

$$f_c=\text{const. (for empirical correction)}\approx 4$$

$$\rightarrow 4 \times c_{PP} \times m_{X1g}$$

Table 4-1 Estimation of the preserved pigment amounts in the analyzed eggshell samples.



Eggshell Specimen	Dromaius novaehollandiae	Heyuannia huangi (Henan)	Heyuannia huangi (Jiangxi)	Heyuannia huangi (Guangdong)
Mass of Fragment [g]	0.187	0.463	0.368	0.289
Amount of PP [nmol]	0.08	0.27	0.14	0.09
Amount of BV [nmol]	4.1	0.23	0.068	0.023
Mass factor (1g) m_{X1g}	5.348	2.160	2.717	3.460
Extraction Correction Factor f_{ex}(PP)	1	1	1	1
Extraction Correction Factor f_{ex}(BV)	3	3	3	3
Empirical Correction Factor f_c	4	4	4	4
Min. PP concentration [nmol/g eggshell]	ca. 2	ca. 2	ca. 2	ca. 1
Min. BV concentration [nmol/g eggshell]	ca. 266	ca. 6	ca. 2	ca. 1
Ratio (BV/PP)	133	3	1	1

4-2-5 Chemical Analysis

We used two commercial standards (biliverdin dihydrochloride and protoporphyrin IX, purchased from Sigma Aldrich), one extant bird eggshell sample (emu), the three fossil *Heyuannia huangi* eggshell samples, and one sediment sample (reddish sandstone) for High Performance Liquid Chromatography coupled to Electrospray Ionization Quadrupole Time-of-Flight Mass Spectrometry (HPLC ESI Q-ToF MS). The basis for this sample selection was (1) to demonstrate reproducibility in three fossil eggshell samples, (2) to exclude the possibility of wholesale contamination due to sample or system exogenous PP or BV input by analyzing sediment adhering to a sample of eggshell, (3) to provide a sensitivity control and quality marker of the analytical routine based on precise detection and quantification of emu eggshell (ranging from the upper (BV) to the lower (PP) detection limit in terms of pigment concentrations), and (4) to generate a calibrated concentration signal for quantification based on the known concentrations of the commercial standards. Adhering sediment and other superficial contaminations were chemically removed from all eggshell samples by a boosted decalcification of the outermost sample surfaces. 500 µL of disodium EDTA solution (100 mg/mL), adjusted to a pH of 7.2, were added to the 180–562 mg eggshell samples and sediment control sample, each of which was stored in 1 mL Eppendorf tube. Samples were incubated for 5 min and then transferred to fresh Eppendorf tubes. The decalcification residue was discarded. Pigment decalcification was performed immediately after preliminary cleaning of the samples. The three oviraptorid eggshell samples, the emu eggshell, and the sediment control sample were incubated again in the EDTA solution which was already used for initial cleaning, this time for 5 min. During this 5 min, the sample tubes were vortexed three times for 1 min. Vortexing was performed with uncapped tubes to allow outgassing of the carbon dioxide generated. After 5 min of incubation in the EDTA decalcification solution, all sample tubes were centrifuged at 15,000 g for 1 min. After centrifuging, the supernatant solutions were collected in separate tubes, while the decalcified sample precipitates were filled up with fresh EDTA solution from the stock. Incubation of 5 min followed, including vortexing 3× in uncapped tubes, as in the previous step. The samples were centrifuged again at 15,000 g for 1 min, supernatants were collected, and the precipitates filled up with fresh EDTA solution. As in the previous step, incubation of 5 min including vortexing of the uncapped sample tubes followed. After a final round of centrifuging for 1 min, supernatant solutions were collected, and the partially decalcified precipitates were used for the final pigment extraction. 1 mL of acetonitrile/acetic acid (4:1, v/v) was added to the decalcified sample pellets for 10 min of incubation, including 2 min of vortex-mixing. Afterwards the sample tubes were centrifuged at 15,000 g for 2 min, and the supernatant solution holding the pigment extract were transferred into fresh Eppendorf tubes, and stored in a dark environment at 4°C. The commercial standards were dissolved in the same acetonitrile-acetic acid solution (4:1, v/v) and stored with the sample pigment extracts. The filtered extracts and commercial standard solutions were stored less than 24 h before they were injected into an HPLC Dionex Ultimate 3000 (Thermo Scientific) separating sample compounds by using an EC50/2 Nucleodur C18 Gravity 3 µm column (MachereyNagel). Reverse-phase HPLC was run at a flow rate of 0.3 mL/min. HPLC was started at 90% H2O containing 0.1% acetic acid. The gradient started after 1 min and reached 100% acetonitrile after 14 min. For an additional 7 min, the column was flushed with 100% acetonitrile (containing 0.1% acetic acid). For the biliverdin analysis, 15 µL sample solution was injected, and 20 µL for the protoporphyrin detection. 2 min of washing runs between each sample extract cleaned the entire system. The liquid chromatography system was coupled to a micrOTOF-Q mass spectrometer (Bruker) with an electrospray ionization (ESI) source inducing positive ionization. Data were collected in positive full scan MS mode over the range of 50–1,000 m/z, using a capillary voltage of 4.5 kV and an end plate offset of −500 V. The dry heater of the ESI source was set at 200°C. Nitrogen desolution and nebulizer gas flow was 10.0 L/min; the nebulizer was run at 2.2 bar. Time-of-Flight (TOF) detection allowed the determination of the accurate masses of biliverdin and protoporphyrin.

4-2-6 Porosity Measurement and Water Vapor Conductance Estimations

We measured eggshell porosity in four eggshell tangential sections of *Heyuannia* egg CYN-2004-DINO-05/I (Figure 4-1A, right egg) under the polarized light microscope using a modification of the zonal division approach (zones 1 to 4, Z_1 to Z_4 in the equation) and asymmetrical egg model applied to troodontid eggs (Varricchio et al., 2013). To take the asymmetrical shape of the oviraptorid egg with its pointed and blunt ends into account, we modelled the shape of the egg as two half prolate ellipsoids and two cones (Figure 4-1B). The blunt end (Z_1) and the acute end (Z_4) were modeled as half prolate ellipsoids with a radius of 4.05 cm and 2.65 cm, respectively, and long axes of equal length (5.7 cm). The rest of the egg between the poles was further divided into two zones (Z_2 and Z_3) which were modelled as two cones (cone height = 4.3 cm and cone radius 4.05 cm and 2.65 cm, respectively). The geometric equations used for calculating egg volume and surface area are given in Table 4-1, as are the regression equations for modern bird eggs that we used for calculating volume, surface area and water vapor conductance of egg CYN-2004-DINO-05/I. The geometric parameters of the model are provided in Table 4-3.

The areas of all individual pores in each tangential section were summed and compared with the total surface area of each zone to calculate the percentage of pore area. This percentage was assumed to apply uniformly to the entire zone and used to calculate the total pore area per zone. Next, the equation (Eq. 4-3) proposed by Jackson et al. (2008) was used to calculate water vapor conductance of the *Heyuannia* egg by zone and overall conductance.

$$G_{H_2O} = \left(\frac{c}{RT}\right) \times D_{H_2O} \times (A_p/L_s) \qquad (4\text{-}3)$$

A_p and L_s are the total pore area and the average pore length, respectively. R represents the universal gas constant which is 6.236×10^4 cm^3 Torr mol^{-1} K^{-1}. T is the temperature in K. c is a conversion factor changing both seconds to days and moles to milligrams of water. c is 1.5552×10^9 sec mg H_2O day^{-1} mol-1. The binary diffusion coefficient of water vapor in air changes with temperature and is 0.292 cm^2 s^{-1} at 30°C. Pore canal length was assumed to be equal to eggshell thickness which is constant for each zone but varies between zones. Accordingly, pore canal length differs in different zones.

The total volume of egg CYN-2004-DINO-05/I is 260.3 cm^2. The egg's weight was estimated as 276 g by applying an average avian egg density of 1.06 g/cm^3 (Deeming, 2006). The G_{H_2O} of an avian egg of equivalent weight is 99.3 mg H_2O day^{-1} $Torr^{-1}$ according to the regression equation proposed by Jackson et al. (2008). This value is slightly lower than our result (108.66 mg H_2O day^{-1} $Torr^{-1}$) (the sum of the values for the four zones in Table 4-3). We compared our results with those published by Mou (1992), which is 231 mg H_2O day^{-1} $Torr^{-1}$ and thus significantly higher than our results. Mou (1992)'s results were also cited by Deeming (2006). The higher values of Mou (1992) result from his assumption that porosity is homogeneously distributed over the entire egg; however, this assumption proved incorrect for elongated eggs (Varricchio et al., 2013). In the Mou's study, several pieces from the middle part of egg were taken for porosity estimation without considering the heterogeneous porosity distribution. Our results (Table 4-3) show that the highest porosity is found in the middle zones, especially in zone 3, which is mainly covered by linearituberculate ornamentation. Hence, the results of Mou (1992) overestimate water vapor conductance mainly because he extrapolated the porosity of the middle part of the egg to the entire egg.

Table 4-2 Geometric equations used for calculating volume and surface area of the fossil egg and regression equations for modern bird eggs used for calculating volume, surface area and water vapor conductance of the fossil egg.

Geometric equations	
Half prolate ellipsoid (for zones 1 and 4)	$V = \frac{2}{3}\pi abc$, for prolate ellipsoid, a=b=4.05 cm (blunt end) or 2.65 cm (acute end). $S = 2\pi\left(a^2+c^2 \times \frac{\epsilon}{\tan\epsilon}\right)$, $\epsilon = \cos^{-1}\frac{a}{c}$ (eccentricity)
Cone (for zones 2 and 3)	$V = \frac{1}{3}\pi r^2 h$, r: the radius of the bottom circle. $S = \pi r(r^2+h^2)^{\frac{1}{2}}$ (Weisstein, 2011) $y = 6.14x - 24.87$ (slope of specific cone used in this model).
Regression equations	
Egg volume	$V_{egg} = 0.51LB^2$, L ≡ egg length, B ≡ egg breadth (Hoyt, 1979).
Egg surface area	$S_{egg} = 4.951\ V^{0.666}$ (Paganelli, Olszowka & Ar, 1974).
Egg conductance	$G_{H_2O} = 0.3786M^{0.818}$, M ≡ egg mass (Jackson et al., 2008).

Table 4-3 Zonal dimensions of the modelled *Heyuannia* egg CYN-2004-DINO-05/I (Figure 4-1A, right egg).

Zone	**Height (cm)**	**% Total egg height**	**Volume (cm^3)**	**% Volume**	**Surface area (cm^2)**	**% Surface area**	**Pore canal length (mm)**
1	5.7	28.5	97.9	37.6	131.95	33.3	1.6
2	4.3	21.5	66.6	25.6	101.28	25.6	1.5
3	4.3	21.5	54.0	20.7	82.12	20.7	1.5
4	5.7	28.5	41.9	16.1	80.62	20.4	1.6

Table 4-4 Results of the porosity measurements and calculations of water vapor conductance of the modelled *Heyuannia* egg CYN-2004-DINO-05/I (Figure 4-1A, right egg).

Zone	Total area (cm^2)	Area examined (cm^2)	No. of pores observed	Pore diameter (µm)	Pore density (no./mm^2)	% Pore area	Pore area, Ap (mm^2)	G_{H_2O} (mg/dayTorr)	Pores per zone	per cm^2 in zone
1	131.95	102	7	56.5	0.069	0.068	9.015	13.77	906	0.104
2	101.28	150	28	57.4	0.187	0.194	19.614	31.95	1891	0.315
3	82.12	342	108	57.2	0.316	0.326	26.789	43.64	2593	0.531
4	80.62	107	17	58.3	0.159	0.170	13.668	20.88	1281	0.259

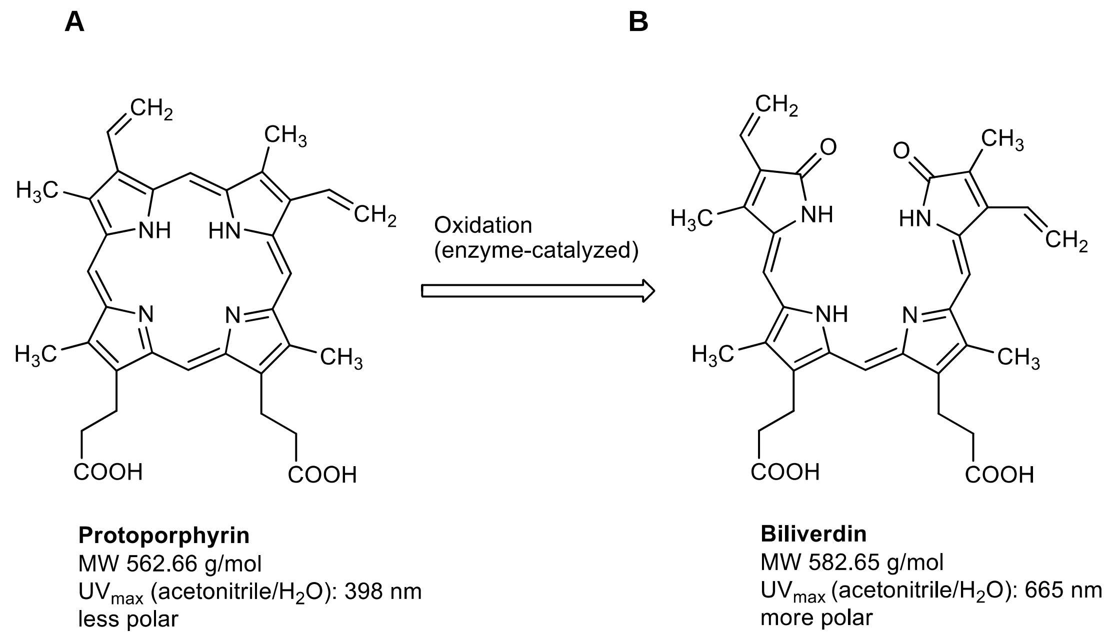


Figure 4-3 Structural formulas of eggshell pigments (A) BV and (B) PP.

4-3 Results

We reliably identified both BV, as [M + H]$^+$ with 583.2520 m/z (calculated mass: 583.2551 g/mol) after 8 min retention time, and PP, as [M + H]$^+$ complex with 563.2623 m/z (calculated mass: 563.2653 g/mol) after 14 min retention time (Figure 4-4A) in the commercial standard solutions, the emu eggshell, and the three fossil oviraptorid eggshell samples. The commercial standard solutions of known concentrations were used to identify the chemotrait-specific, diagnostic retention times for BV and PP on the chromatographic column. Elution of BV was consistent after 8 min, while elution of PP delayed consistently until 14 min of the run mobile phase gradient (consistent with Igic et al., 2010). A second compound-diagnostic trait was provided by ionization after elution from the chromatographic column, followed by exact mass determination of the [M + H]$^+$ ion complexes. Differing behavior of BV and PP native to eggshells compared to commercially purified BV and PP was ruled out by identical retention times, number of isoforms/tautomers, and exact mass peaks of emu eggshell BV and PP and the commercial standard solutions. Furthermore, maximum sensitivity of the HPLC ESI MS system was demonstrated by precise detection of pigment concentrations in the emu eggshell solution which approached the upper (BV) and the lower (PP) detection limits. The extracted ion chromatograms (EICs) for BV and PP obtained from the sediment sample whole ion mass spectrum yielded signals within broader tolerances of the BV and PP exact masses, but no peaks corresponding to the commercial standard calibrated retention times were identified. Absence of a diagnostic mass peak after 8 min retention time on the column for BV, and after 14 min retention time on the column for PP, is a significant demonstration of absence of trace amounts BV and PP in the sediment sample. Thereby, contamination of the samples or the detection system was excluded and originality of the detected pigments in the oviraptorid eggshell samples is guaranteed. Quantification of the detected pigment concentrations based on commercial standard calibration was determined by application of an experiment-empirical correction for the extraction loss of BV due to its increased hydrophily of the fossil oviraptor eggs. We found the highest preserved concentrations of BV in the eggshells from Henan (6 nmol/g), followed by the eggshells from Jiangxi (2 nmol/g) and those from Guangdong (1 nmol/g). The preserved PP concentrations ranged from 2 nmol/g in both the Henan and Jiangxi eggshells to 1 nmol/g in the Guangdong eggshells. Our empirical correction applied to the fossil eggshell samples yielded very realistic pigment concentration estimates for the emu eggshell of 2 nmol/g PP, and 266 nmol/g BV which fall into the reported range of emu eggshell pigment concentrations in the scientific literature (Table 4-1). The bluish shimmer of the fossil oviraptorid eggshells suggests generally higher BV concentrations than those we detected, as also found in a similar study on pigment preservation in subfossil moa eggshells using the same methodology. The color of the fossil eggs suggested higher BV concentrations than the authors managed to detect. Taken together, our study and the study by Igic et al. (2010) imply that bluish or greenish coloring degradation products of BV remain which therefore shows slightly different chemical properties and different exact masses and is thus not detected by an LC MS system targeting unmodified compounds measurable against commercial standards. To demonstrate the perceivability of a visual color signal based on the detected pigment concentrations in the oviraptorid eggshells, we plotted our pigment concentrations into the comprehensive pigment concentration-color matrix of (Cassey et al., 2012). Our three dinosaur egg color data points fall in the visibly olive-green color range between *Haliaetus albicilla* and *Circus aeruginosus* (Cassey et al., 2012). They plot in the cluster of unspotted eggs, suggesting an immaculate, homogenous coloration. No patterns were visible in the fossil eggs (Figure 4-1). Since the preserved fossil oviraptor eggshell color suggests originally higher BV concentrations, taphonomy needs to be considered to generate a realistic, native oviraptor egg color reconstruction. Because BV is more reactive and more hydrophilic, and thus soluble in sediment-percolating aqueous fluids, the concentrations of unmodified, preserved pigments after at least 66 million years of sedimentary burial are much more likely to be significantly lowered than those of the more stable, hydrophobic PP (Falk, 1964). Therefore, the taphonomic projections of our preserved pigment concentrations in the avian egg color space (Cassey et al., 2012) realistically lift the investigated oviraptor egg colors significantly towards much higher BV values, while the shift towards increased PP values would be only minimal. However, our fossil oviraptor eggs would remain deeply nested within the area of unspotted eggs (based on Cassey et al., 2012). Such an additional taphonomic correction of the reconstructed egg color approximates an intensively blue–greenish oviraptorid egg color. Whether the differences in preserved pigment concentrations between the three fossil oviraptor egg samples from different localities reflect intraspecific variation in egg color or different taphonomic conditions in the deposits cannot be reliably assessed at this point and requires future investigations. Since these differences in preserved pigment concentrations in the oviraptorid eggshells affect the BV values much stronger (range 6–1 nmol/g) than they affect the PP values (range 2–1 nmol/g), we assume that differences in color are more likely to be taphonomic. In vivo intraspecific variation of egg color would most likely affect BV and PP concentrations equally, while taphonomic effects affect BV concentrations much stronger than PP concentrations (Falk, 1964). Also, the original egg color is overprinted by a generally blackish-brownish hue (Figure 4-1). This brownish discoloration traces back to preserved, oxidatively crosslinked eggshell organic matrix proteins of the AGE/ALE-type (Wiemann et al., 2016). Our reconstruction of colored eggs for oviraptors is consistent with our reevaluation of the oviraptorid nesting mode: we consider oviraptor eggs as lying at least partially open in the nest (consistent with Norell et al., 1995). This reconstruction is based on the estimated water vapor conductance of 108.66 mg H2O day^{-1} Torr^{-1} for the *Heyuannia* egg NMNS CYN-2004-DINO-05/I from the province of Jiangxi (Figure 4-1A). This value is calculated from the four zonal conductances deduced from zonal porosity counts (section 4-2-6). The highest values for shell porosity were found in the middle portion of the oviraptor egg (zones 2 and 3), and especially pronounced in zone 3 with a resultant conductance of 43.6 mg H_2O day^{-1} Torr-1 (Table 4-3). The pointed end (zone 4) which is stuck in the nest material, has a calculated conductance of 22.88 mg H_2O day^{-1} Torr^{-1}, while the exposed blunt end (zone 1) has a calculated conductance of 13.77 mg H_2O day^{-1} Torr^{-1} (Table 4-3).

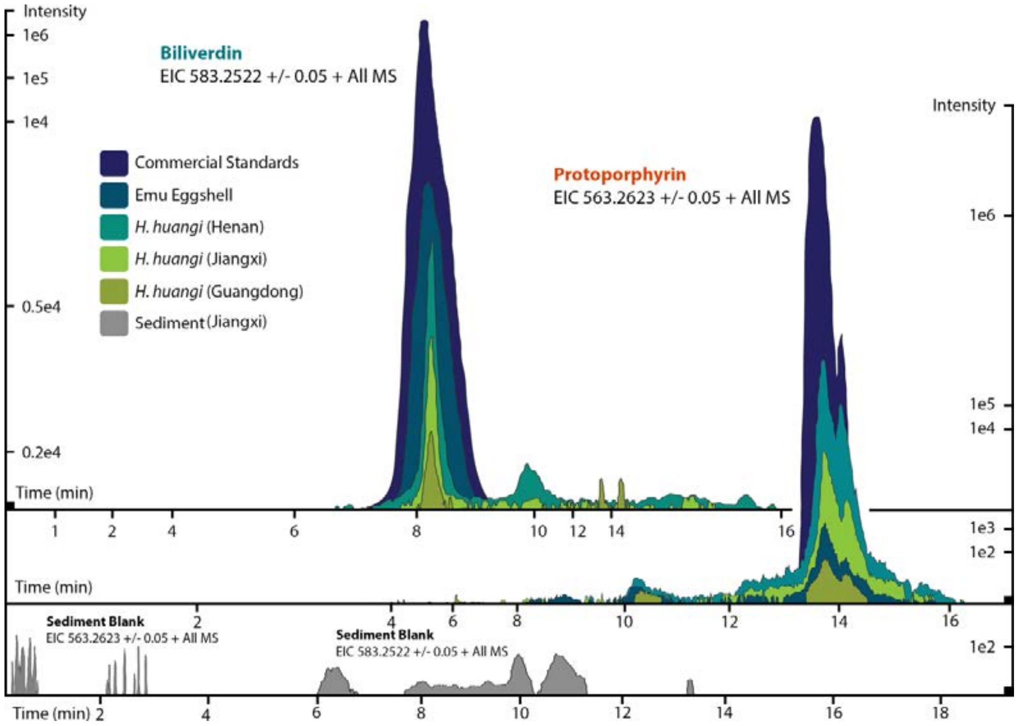


Figure 4-4 ESI (+) MS extracted ion chromatograms (EICs) for mass 583.2520 ± 0.01/0.05 m/z, indicative of BV, and mass 563.2653 ± 0.01/0.05 m/z, indicative of PP. We identified BV and PP by retention time, exact mass and isoform/tautomer separation. EICs for 583.2520 ± 0.01/0.05 m/z are depicted for the commercial BV standard, emu eggshell, extracts of *Heyuannia huangi* eggshells derived from the Chinese provinces Henan, Jiangxi, and Guangdong and the sediment control extract from Jiangxi. Unmodified BV elutes after 8 min retention time, and was proven present for the biliverdin commercial standard, the emu eggshell, and the three oviraptorid eggshells. The sediment sample was used as control for contamination, and its EIC does not show a peak after 8 min retention time, proving the absence of biliverdin in the sediment sample and the originality of biliverdin detected for the eggshell samples. EICs for 563.2653 ± 0.01/0.05 m/z are depicted for the commercial PP standard, emu eggshell, *Heyuannia huangi* eggshell derived from the Chinese provinces Henan, Jiangxi, and Guangdong, and the sediment sample from Jiangxi. Unmodified PP elutes after 14 min and was proven present for the PP commercial standard, the emu eggshell, and the fossil oviraptorid eggshells. There is no peak in the PP EIC for the sediment sample after 14 min, what proves the absence of PP in the sediment control sample, and the originality of PP in the eggshell samples. Peak intensity correlates with pigment concentrations in the extracts.

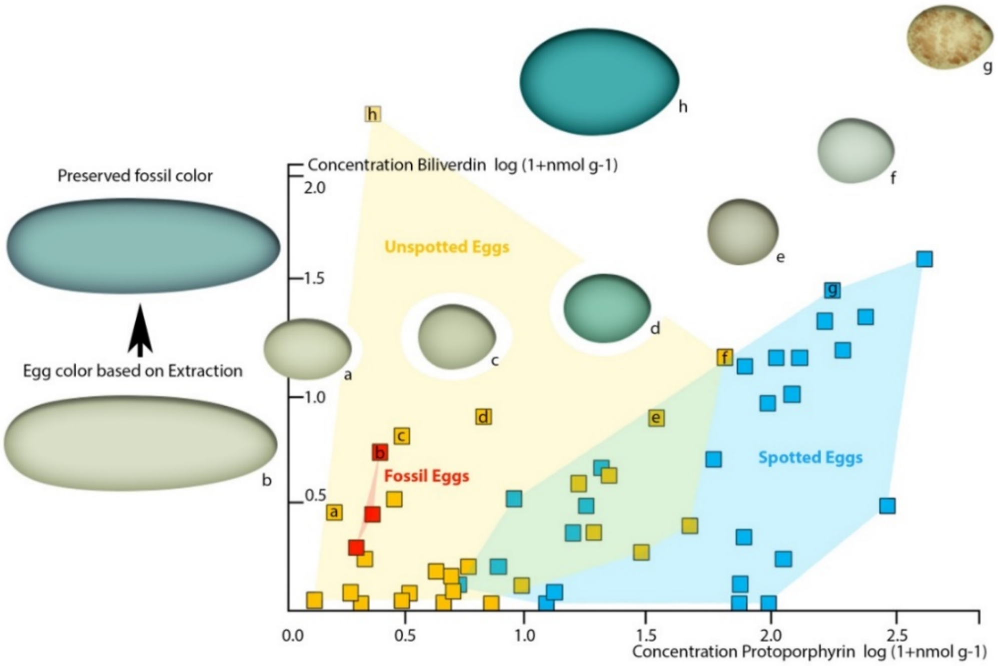


Figure 4-5 Plot of oviraptor egg and different avian egg biliverdin concentrations against their protoporphyrin concentrations with example for the overall color impression based on the dataset published by Cassey et al. (2012). Avian eggs cluster together moderately separated into unspotted (yellow cluster, yellow squares) and spotted (blue cluster, blue squares) eggs. Fossil oviraptorid eggs span a color space (red cluster) and are represented by red squares, all nested within definitely unspotted eggs. The color examples extracted from Cassey et al. (2012) indicated for the preserved oviraptor egg pigments concentrations a visibly olive-green color (framed by a: *Haliaetus albicilla*; c: *Circus aeruginosus*). This color estimate lies still below the preserved bluish shimmer of the eggshells. Egg colors at cluster edges are extracted from Cassey et al. (2012) and labelled from a – h.

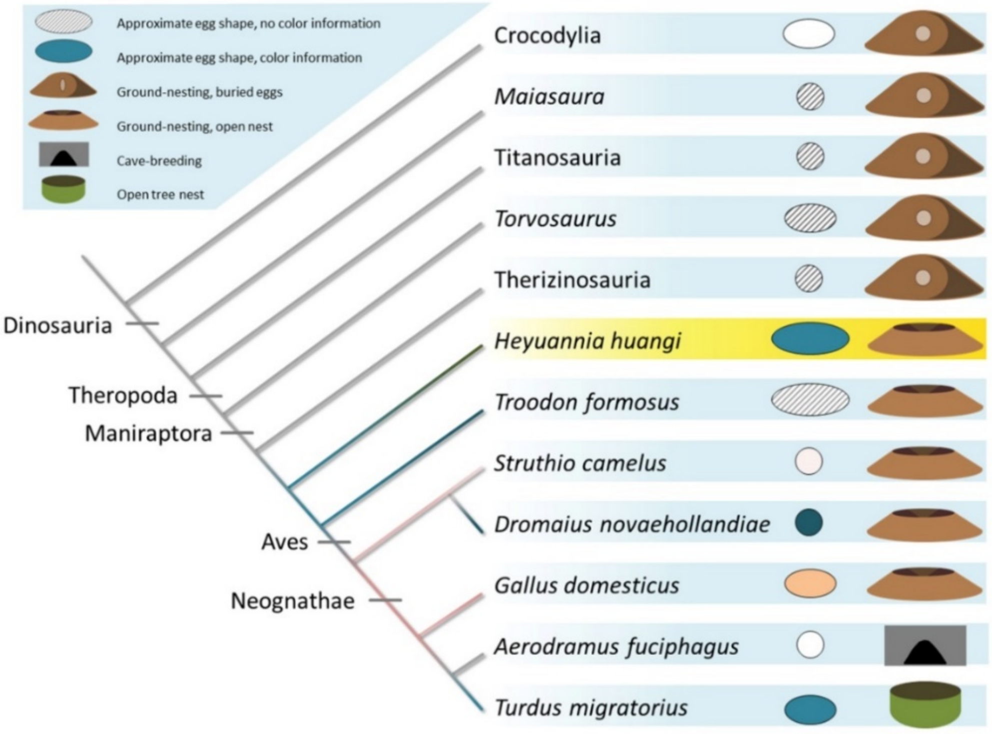


Figure 4-6 Evolution of egg coloration (egg item), egg shape (egg item), and nesting type (nest item) in archosaurs. Listed (as successive outgroups) are ornithischian dinosaurs, such as *Maiasaura*, for sauropods, such as titanosaurs, and theropod dinosaurs, including *Torvosaurus*, therizinosaurs, oviraptors, troodontids, and crown birds (Varricchio & Jackson, 2016). The topology of the tree is based on Nesbitt (2011) (Archosauria), Sereno (1999) (Dinosauria), Carrano, Benson & Sampson (2012) (Tetanurae), Turner, Makovicky & Norell (2012) (Paraves), Prum et al. (2015) (Aves). Porosity data and clutch structure indicate a fully buried nesting type for most dinosaur taxa Varricchio & Jackson (2016). Buried eggs which are indicated by the nesting item next to the egg item for each terminal taxon appear to be plesiomorphic. Oviraptorid dinosaurs, here represented by *Heyuannia huangi*, built at least partially open nests, concurrent with the phylogenetically most basal appearance of PP and BV in dinosaur eggshell (egg item). In modern birds, eggshell pigmentation varies with nesting microenvironment. Presence and kind of the (more abundant) eggshell pigment is represented by the color of the cladogram branch, and the egg item next to each terminal taxon. Beige egg colors indicate PP being more abundant, whereas bluish egg colors indicate BV being more abundant.

4-4 Discussion

4-4-1 Paleoecological Implications

Some aerobic microorganisms are known to produce protoporphyrin as an intermediate of their cytochrome c biosynthesis, and they also use biliverdin which represents a highly-conserved metabolite. Thus, a microbial origin of the pigments that we detected from our oviraptorid egg samples needs to be excluded. We use the double-checking LC MS approach (based on Gorchein, Lim & Cassey, 2009) applied to sediment adherent to the oviraptorid eggshells from Jiangxi to reliably exclude any wholesale sample contamination, contamination of the LC MS system, of used laboratory equipment or chemicals. Absence of any traces of BV or PP in our sediment control sample proves the cleanliness of our analytical system and supplies, as it proves absence of whole sample contamination based on potentially abundant microbes in the deposits. The only alternative source of the detected oviraptorid eggshell pigments would be eggshell-only contamination with microbially derived BV and PP (Woodard & Dailey, 1995). The preserved bluish-greenish shimmer of the investigated eggshells strongly argues against this. Also, the preserved pigment concentrations and differing BV and PP ratios eliminate the possibility of eggshell-only microbial contamination. The preserved concentrations fall within the empirical correction for pigment loss during the extraction routine (see Figure 4-4). Thus, the most parsimonious conclusion is that we have documented oviraptorid eggshell pigments.

Our results push the origin of pigmented eggshells phylogenetically back to oviraptorid dinosaurs (see Figure 4-5; Kilner, 2006). To test for convergent evolution or homology of egg color between oviraptorids and crown birds, future investigations of pigmentation in other eumaniraptoran eggshells are required. Oviraptorid dinosaurs incorporated the same pigments and isoforms into their eggshells, out of a pool of dozens of possible staining secondary metabolites (McGraw, 2006; Hubbard et al., 2010; Stoddard & Prum, 2011). If dinosaur egg color was a convergent character relative to the colored eggs of crown birds, the same color effect could have been achieved by use of different metabolites. Non-avian dinosaurs and modern birds apparently use the same molecules to create eggshell coloration. There are no studies available testing for pigment constraints during the shell formation based on simultaneous shell crystallite growth and pigment incorporation into the eggshell organic matrix. Also, potential constraints of metabolite transport mechanisms or de novo synthesis sites in the archosaur shell gland are yet unknown, as is metabolite permeability through the archosaur shell gland wall. In any case, we can infer based on our results that oviraptor shell glands generally worked in a similar way as avian shell gland does: due to its hydrophilic behavior biliverdin is preferentially incorporated into the organic matrix of the eggshell prismatic zone which holds the calcite crystallites (Falk, 1964). Biomaterial studies suggested thioether linkage of BV to cysteine-rich proteins, allowing an energy-efficient storage close to the ion lattice of calcite crystals (Lamparter et al., 2004; Salewski et al., 2013). Based on this presumably general storage mechanism of BV in biocomposite materials, we infer a similar storage in oviraptor eggshells. PP is secreted during the final steps of eggshell formation, while the storage mechanism is yet unclear. Due to its hydrophobic properties, PP is currently thought to occur in highest concentrations in the waxy eggshell cuticle (Baird, Solomon & Tedstone, 1975). Thus, evidence for PP in fossil oviraptorid eggshells strengthens the support for hypothesized preservation of eggshell cuticle through deep time (Mikhailov, 1991; Schweitzer et al., 2002; Varricchio & Jackson, 2004). Both pigments are supposed to be synthesized de novo in the shell gland tissue (Wang et al., 2009).

Combining our pigment analyses with the outcomes of studies on oviraptorid clutch arrangements (Huh et al., 2014; Pu et al., 2017), it can be summed up that oviraptorid eggs were most probably laid in overlapping circles, partially stuck in the nesting material, with their blunt ends exposed, pointing upwards in an almost vertical orientation. Partially exposed, blue-green eggs, stacked in circular layers, allow the inference of a similarly colored nesting material. In modern birds, blue-green eggs stored in ground nests are found in Casuariformes, including emus and cassowaries (Coombs & Farlow, 1989). Emus and cassowaries lay their eggs in soil mounds covered with leaf litter and vegetation, so that egg color and nesting background match in tone (Coombs & Farlow, 1989). Considering arid to subtropical paleoclimate reconstructions for Late Cretaceous China (Hsu, 1983), and the fluvial/alluvial red silt-sandstone sedimentology of the fossil laegerstaetten from Henan, Jiangxi and Guangdong provinces, vegetation coverage of the nest base comparable to emu and cassowary nests, adjacent to permanent or rather ephemeral river systems would offer an environment requiring blue-greenish egg colors for nest crypsis. An alternative explanation to only cryptic functions of blue-green eggs has been described for tinamous (*Tinamus major*): blue-green eggs in tinamous (*Tinamus major*) have been demonstrated to be non-cryptic and to be laid in environments where the egg color significantly contrasts the nesting background color (Brennan, 2010). In tinamous, nest predation depends not on egg color cues, but mainly on either visual or chemical parental cues during clutch incubation, and egg color is supposed to have evolved for intraspecific signaling (Brennan, 2010). Intraspecifically, blue-green egg color in modern birds has been associated with paternal care, communal nesting, and postmating sexual signaling (Handford & Mares, 1985; Moreno & Osorno, 2003). Paternal care was previously hypothesized to have dinosaur origin, tracing back to oviraptorid dinosaurs, and thus, poses a good fit our finding of oviraptorid blue-green egg color (Varricchio et al., 2008, but see Birchard, Ruta & Deeming, 2013). Communal nesting, as seen in polyandrous birds like emus and cassowaries, represents a reproductive strategy that might apply for non-avian dinosaurs, but has never been tested for (Handford & Mares, 1985). Preliminary studies based on eggshell chemical signatures identifying multiple maternal individuals contributing eggs to one clutch hint at communal nesting in oviraptorid dinosaurs (Yang et al., 2016). Finally, postmating sexual signaling according to the Sexual Signaling Hypothesis appears controversial in the ornithological literature (Moreno & Osorno, 2003; Krist & Grim, 2007). This hypothesis suggests intensive blue-green egg color as a quality marker for maternal health and immunocapability (Moreno & Osorno, 2003). Post-mating sexual signaling then occurs due to BV being incorporated in high concentrations into the eggshell because it is dispensable to the maternal metabolism (Moreno & Osorno, 2003). The general idea goes back to the handicap hypothesis (Roberts, Buchanan & Evans, 2004), and assumes that the male is motivated by the confirmation of the female health status and thus, the offspring quality (Moreno & Osorno, 2003).

The similarity in reproductive strategies between crown birds and derived non-avian maniraptorans may reflect shared selective pressures: the recent discovery of the anseriform *Vegavis* in Late Cretaceous deposits from Antarctica provides evidence that crown birds coexisted with non-avian dinosaurs (Clarke et al., 2016). The presence of neognath birds in the Late Cretaceous implies that paleognath birds already diverged at this point (based on avian phylogeny by Prum et al., 2015). We would like to suggest new avenues of research based on the perspective of the potential coexistence, shared selection pressures, and niche competition of secondarily flightless paleognath birds and oviraptorid, dromeosaurid, and troodontid dinosaurs.

4-4-2 Cuticle Preservation

In extant bird eggs, the cuticle layer is composed of an inner calcified layer and an outer non-calcified layer. The inner calcified layer consists of a thin layer of hydroxyapatite (Dennis et al., 1996). Eggshell from an embryo-bearing *Heyuannia* egg (NMNS-0015726-F02-embryo-01) was radially sectioned for observation under a polarized light microscope. In the radial section of this eggshell specimen, we observed a mineralized layer with mammillae-like structures atop the crystalline layer of the eggshell, which may be the preserved inner hydroxyapatite layer of the original cuticle (Figure 4-7). This observation is consistent with the detection of PP because PP is mainly deposited in the cuticle.

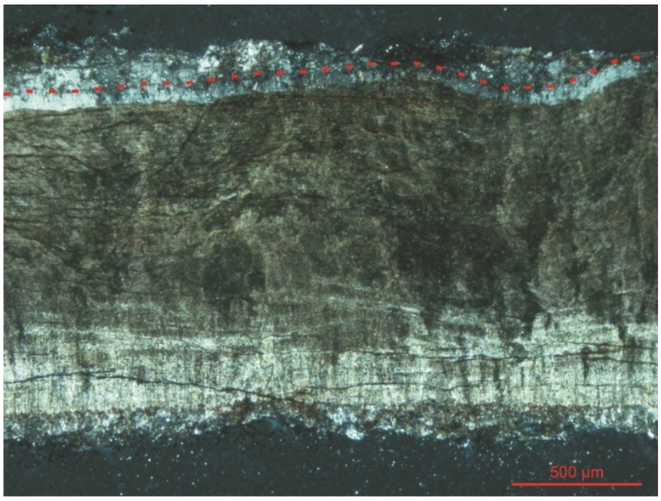


Figure 4-7 Radial section of eggshell from an embryo-bearing *Heyuannia* egg (NMNS-0015726-F02-embryo-01) in polarized light showing the putative cuticle layer below the red dashed line and the outer surface of the brownish crystalline layer. Scale bar equals 500 µm.

4-5 Conclusion

Our study extends the origin of colored eggs from crown birds to oviraptorid dinosaurs. The result has important implication both for the origin of avian biology and the reproductive biology of theropods dinosaurs. This work also broadens the scope of paleontological research on molecular preservation and ecology to hard vertebrate tissues. Our study ties together previous hypotheses on the eumaniraptoran origin of partially open nesting, and paternal care. Also, potential future avenues for investigation are posed by the potential linkage between blue-green egg color and communal nesting, as well as polyandry, which represent yet unaddressed topics in extinct archosaurs.

The second aspect of our work focuses on its implications for molecular and soft tissue preservation through deep time. Chemically stable, relatively small biological molecules such as PP and BV appear to be protected from complete degradation over millions of years in carbonate biomineral matrices, in an oxidative sediment milieu. Similar biomolecule preservation may also be present in enamel, dentine and bone mineral. Ancient biomolecules and the soft tissues which they construct pave the way to trace life and its behaviors through time and, thus, invite further studies since they are easily detectable, more abundant than expected, and revolutionary in their ecological implications.

Chapter 5 Reconstruction of oviraptorid clutches illuminates their unique nesting biology

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PUBLICATION

Yang T-R, Wiemann J, Xu L, Cheng Y-N, Wu X, and Sander PM. Reconstruction of oviraptorid clutches illuminates their unique nesting biology. (accepted by Acta Palaeontologica Polonica) (with some modifications)

ABSTRACT

Oviraptorosaurs, a group of non-avian theropod dinosaurs from the Cretaceous of Asia and North America, yield the most abundant fossil record that elucidates their reproductive biology. In the aspect of reproductive biology, previous studies suggested that oviraptorosaurs represent an intermediate stage that have exhibited unique modern avian traits. For instance, the adult-associated clutches were predominantly considered as evidence for brooding/thermoregulatory contact incubation (TCI) behaviors, whereas the hypotheses of laying or protection were neglected. Despite numerous oviraptorid egg clutches uncovered from China and Mongolia, their nest architecture and clutch arrangement were never investigated in detail. Here we present a comprehensive reconstruction of an oviraptorid clutch based on five new oviraptorid clutches from Jiangxi Province, China. A detailed examination of the new clutches reveals a partially-open oviraptorid nest that contains 3-4 rings of paired eggs (more than 15 pairs) whose blunt end points toward the center devoid of eggs at an angle of 35° to 40°. Evidence arising from our reconstruction indicates that an oviraptorid nest shows unique architecture and egg arrangement unanalogous to extant bird's clutches, implying an apomorphic nesting mode in oviraptorids. Such a peculiar nest architecture further contradicts the TCI hypothesis in oviraptorids, hindering sufficient heat transfer to the inner(lower) ring(s) of eggs. Moreover, the size of new oviraptorid clutches (>30) is significantly larger than that of the adult-associated clutches (<22), raising the alternative hypothesis

that the adult-associated clutches were uncompleted. This clue thus supports the hypothesis that the clutch-associated oviraptorid adults possibly represent females after an oviposition before a catastrophic sandstorm/flooding burial.

5-1 Introduction

5-1-1 From a Thief to a Loving Mom

Oviraptor, which means "egg thief", was named by Osborn in 1924 based on the *Oviraptor philoceratops* (AMNH FARB 6517, Figure 5-1A) and its associated clutch (AMNH FARB 6508, Figure 5-2B) from the Late Cretaceous (Campanian) Djadokhta Formation of Bayn Dzak (= the Flaming Cliffs = Shabarakh Usu), Mongolia (Osborn, 1924). Osborn assigned the associated clutch to protoceratopsians and hence proposed the hypothesis that oviraptors preyed on proceraptopsian eggs. Seventy year later, Norell et al. (1994) described an embryo-containing egg (IGM100/971) from the Djadokhta Formation of Ukhaa Tolgod, which exhibited striking morphological similarity to those "protoceratopsian" eggs of the 1924 clutch, but contained cranial remains presenting diagnostic features associated with oviraptorids. Therefore, the hypothesis that oviraptors were egg thieves was mute. Subsequently, Norell et al. (1995) reported another oviraptor adult-associated clutch from Ukhaa Tolgod and suggested a bird-like "brooding" behavior (Figure 5-2). This implied the origin of bird-like incubation in basal maniraptorans and gave rise to an entire branch of research investigating the origins of avian characters in their non-avian dinosaur stem. Since 1995, two other similar specimens were discovered and interpreted as "brooding" clutches as well: IVPP V9608 from the Djadokhta Formation of Bayan Mandahu, Inner Mongolia, China (Figure 5-3; Dong & Currie, 1996; Longrich, Currie & Dong, 2010), and IGM 100/1004, again from Ukhaa Tolgod (first reported by Clark et al., 1999 and re-described by Norell et al., 2018) . The specimens IGM 100/979 and IGM 100/1004 were used to erect the new taxon *Citipati osmolskae* in 2001 (Clark et al., 1999; Clark, Norell & Barsbold, 2001). Fanti, Currie & Badamgarav (2012) described an 18-egg clutch from the Baruungoyot Formation of the Nemegt Basin, southern Mongolia (MPC-D 107/15, Figure 5-4), which lacks a clear clutch patterning due to poor preservation, again with a partial skeleton in brooding position on top, and suggested the new taxon *Nemegtomaia barsboldi* based on this material. Most recently, two new oviraptor associated-clutches (Figure 5-5 & Figure 5-6) were excavated, for the first time, from the fluvial deposits of Nanxiong Formation in Jiangxi, southern China (one of them was preliminarily described by Bi & Xu (2017).

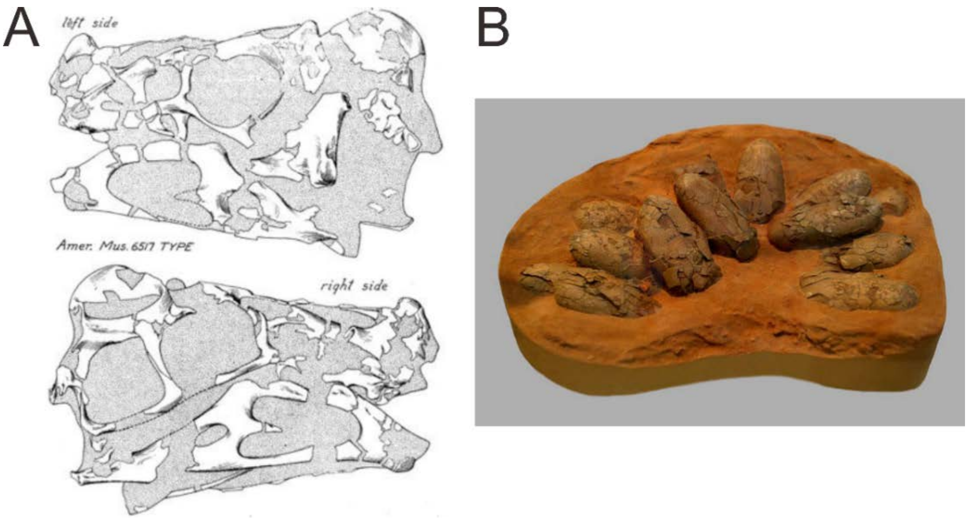

Figure 5-1 The holotype of *Oviraptor philoceratops*. (A) Illustrations of the holotype *Oviraptor philoceratops* from left and right side-views and (B) photograph of its associated clutch (AMNH 6517 and AMNH 6508; Osborn, 1924; http://research.amnh.org/paleontology/media/images/). The clutch was prepared from the bottom.

Figure 5-2 Photograph of the "brooding" oviraptorid specimen (IGM 100/979) described in Norell et al. (1995). This specimen consists of an avian-like sitting adult and an egg clutch estimated to encompass 22 eggs. Only 15 eggs are exposed since the other eggs beneath the skeletons cannot be exposed without removing the skeletons. Note that the eggs were crushed by sediment compaction, but still retain a paired arrangement. The eggs are arranged in two nearly concentric rings, four in the upper ring (beneath the right forelimb) and eleven in the lower ring, respectively. The blunt ends of the eggs point to the center devoid of eggs. Scale bar: 10 cm. Reprinted with permission from Macmillan Publishers Ltd: [NATURE] [1], copyright (1995).

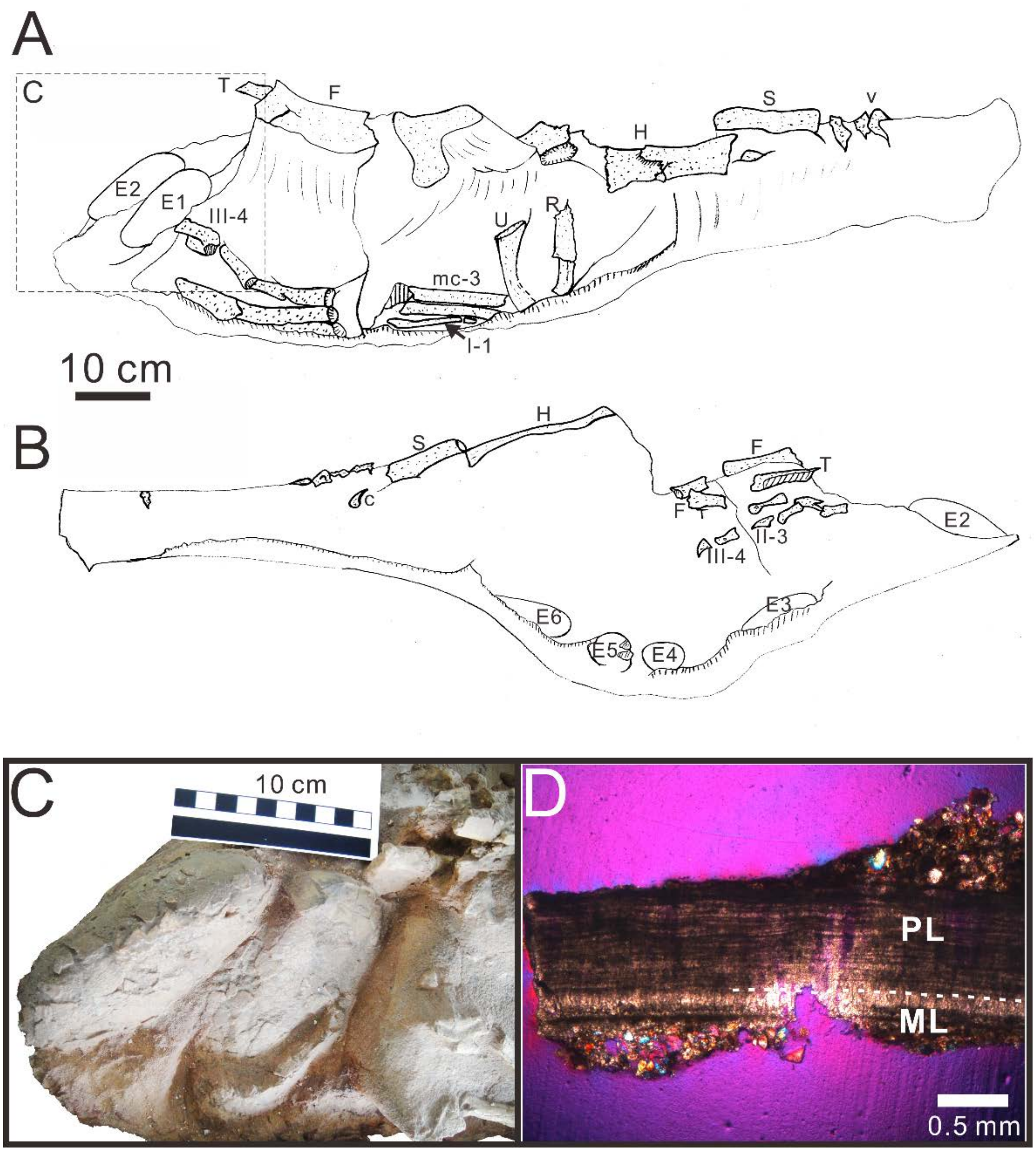

Figure 5-3 A partial oviraptorid preserved with six eggs housed in the IVPP (IVPP V9608) first described by Dong & Currie (1996). (A) Right lateral sketch of IVPP V9608. The blunt end of both eggs (E1 and E2) under the tibia points inward, indicating a similar arrangement of eggs as in IGM 100/979. (B) Left lateral sketch of IVPP V9608. Two eggs (E4 and E5) point inward underneath the humerus and femur. (C) Detail of E1 and E2 in the dashed region of (A). Note that the eggs are crushed due to sediment compaction. (D) Petrographic thin section of the eggshell from specimen IVPP V9608 under the polarizing microscope. The mammillary layer (ML) is intact, implying that little erosion on the innermost eggshell occurred before fossilisation. The white dashed line marks the boundary between the prismatic layer (PL) and mammilary layer (ML). c, clavicle; E: egg; F, femur; H, humerus; R, radius; S, scapula; T, tibia; U, ulna; v, vertebra; mc3, metacarpal 3.

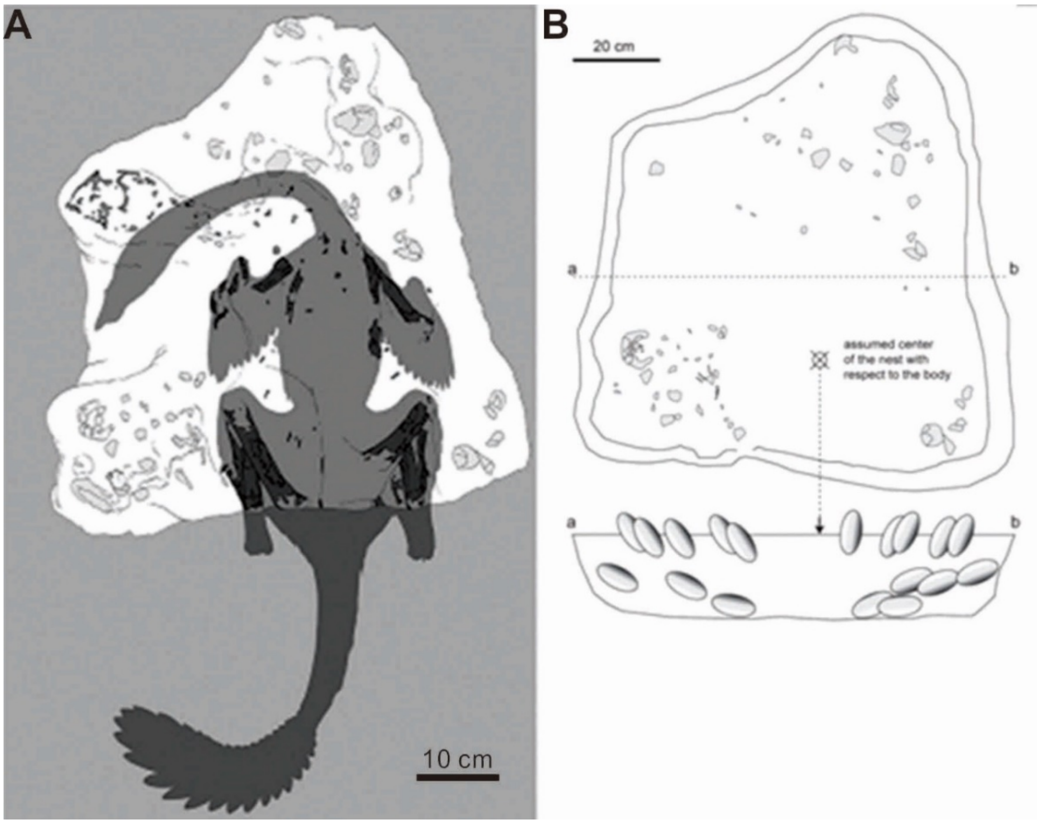

Figure 5-4 Photograph of the brooding *Nemegtomaia barsboldi* (MPC-D 107/15; Fanti, Currie & Badamgarav, 2012). The MPC-D 107/15 specimen was discovered from the Baruungoyot Formation in Mongolia. (A) The MPC-D 107/15 block and the simulated sitting oviraptor on the egg-clutch. The eggs, the arrangement of the eggs, and the architecture of the egg-clutch are poorly preserved, showing only an indistinct configuration of the nest. Both of hindlimbs are preserved as like curling legs, suggesting an avian brooding gesture of the adult on the egg-clutch. Scale bar: 10 cm. (B) The specimen was prepared from the bottom. However, Fanti, Currie & Badamgarav (2012) did not address that the side pointing to the center is the blunt end, which is a crucial observation for identifying the top or bottom of the specimen. Reprinted from Fanti, Currie & Badamgarav (2012). Scale bar: 20 cm.

Figure 5-5 Photograph of an undescribed brooding specimen (AGB 4990). This specimen was discovered in Ganzhou, Jiangxi Province, China, currently housed at Anhui Geological Museum in Hefei, China.

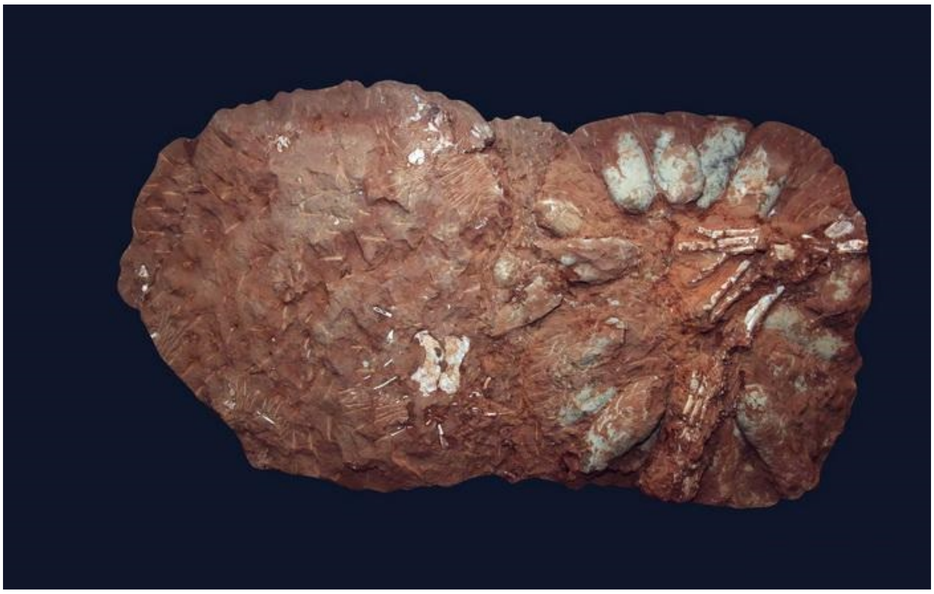

Figure 5-6 Photograph of an undescribed brooding specimen from Ganzhou, Jiangxi Province, China. This specimen has been briefly reported by Bi & Xu (2017). Reprinted from Zhejiang Museum of Natural History, Hanzhou, Zhejiang Province, China (http://www.zmnh.com/html/7961.htm).

Thus, to date at least seven oviraptorid clutches topped by an adult individual have been discovered, including five from the sand-dune deposits in Mongolia and China and two from the Nanxiong Formation in southern China (Table 5-1). The ones from the sand-dune deposits in Mongolia and China represent four separate taxa of oviraptorosaurs (Table 5-1; Osborn, 1924; Norell et al., 1995; Dong & Currie, 1996; Clark et al., 1999; Fanti, Currie & Badamgarav, 2012; Norell et al., 2018). In the wake of these discoveries of adult-associated specimens, the body heat-incubation/brooding hypothesis appears to have progressively gained more acceptance over the egg-laying hypothesis, following a surge of discoveries of feathered dinosaurs in northeastern China and Canada, which traced more and more avian features back to their dinosaur ancestors (Ji et al., 1998). Recently, the heat-incubation/brooding hypothesis was also obscurely imposed on other oviraptorosaurian taxa, such as *Beibeilong* (Pu et al., 2017) and an unknown taxon (Amiot et al., 2017); however, without previous reports on clutch-associated adults of these taxa. Therefore, a rigorous discussion for different types of brooding is crucial for further detailed discussion of "brooding behavior" in oviraptorids later.

In modern birds, the term "brooding" covers the two categories "prehatching brooding" and "posthatching brooding" (Mandal, 2012). For dinosaurs, previous studies mainly discussed "prehatching brooding" (Osborn, 1924; Norell et al., 1995; Dong & Currie, 1996; Clark et al., 1999; Fanti, Currie & Badamgarav, 2012; Norell et al., 2018), while "posthatching brooding" was rarely discussed. Posthatching brooding comprises protecting and taking care of the young after hatching, and also includes body heat transfer from the adult to the hatched offspring. Prehatching brooding involves incubation behavior, which means the adult is sitting on the eggs to keep them warm and to bring them to hatching. In altricial birds, endothermy develops in the chicks only after hatching, which is why they are thermally dependent on brooding adults for the first days after hatching (Dawson, Bennett & Hudson, 1976; Whittow & Tazawa, 1991; Hohtola & Visser, 1998). In superprecocial and precocial birds, endothermy is gained even before hatching, (Whittow & Tazawa, 1991). Since altricial bird embryos and hatchlings show a strong allometry of skull, wing, and hindlimb proportions, freshly hatched chicks are rather immobile, which forces them to remain in their nest at least for some time (Whittow & Tazawa, 1991). More precocial birds have already well developed walking legs and musculature and are thus not that limited in their locomotion (Whittow & Tazawa, 1991). Precocial birds do not need as much "post-hatching" parental care as altricial birds do. Furthermore, adults usually "brood" their hatchlings during the first days after hatching also to protect them from predation (Dial, 2003; McLennan et al., 2004).

Table 5-1 Specimen number, clutch size, number of rings, taxonomic assignment, locality information, and stratigraphic horizon of the previously described "brooding" specimens and the unreported specimens.

Specimen number	Clutch size	Number of rings	Taxonomic assignment	Locality information	Stratigraphic horizon and references
AMNH 6508 AMNH 6517	15	2	*Oviraptor philoceratops*	Bayn Dzak (The Flamming Cliffs=Shabarakh Usu), Mongolia	Djadokhta Formation (Figure 5-1; Osborn, 1924)
IGM 100/979 (Big Mamma)	15 (visible) 22 (estimated)	2	*Citipati osmolskae*	Ukhaa Tolgod, Mongolia	Djadokhta Formation (Figure 5-2; Norell et al., 1995)
IGM 100/1004 (Big Auntie)	Not reported	2	*Citipati osmolskae*	Ukhaa Tolgod, Mongolia	Djadokhta Formation (Clark et al., 1999; Norell et al., 2018)
IVPP V9608	6	1	cf. *Machaisaurus*	Bayan Mandahu, Inner Mongolia, China	Djadokhta Formation (Figure 5-3; Dong & Currie, 1996; Longrich, Currie & Dong, 2010)
MPC-D 107/15	18	2?	*Nemegtomaia barsboldi*	Nemegt, Mongolia	Baruungoyot Formation Figure 5-4; Fanti, Currie & Badamgarav, 2012)
AGM 4990	30	3	?	Ganzhou, Jiangxi, China	Nanxiong Formation (Figure 5-5; unpublished work)
Uncatalogued	9	1	?	Ganzhou, Jiangxi, China	Nanxiong Formation (Figure 5-6; Bi & Xu, 2017)

Norell et al. (1995) described the sitting oviraptor only as a "brooding" rather than an "incubating" adult. However, their description suggested the association between brooding behavior and incubation by heat transfer from the adult (thermoregulatory incubation). This view of brooding oviraptorids has been challenged by paleontologists and ornithologists for over 20 years (Carpenter, 1999b; Deeming, 2002a; Ruben, Jones & Geist, 2003; Jones et al., 2012). Horner (2000) also pointed out that Norell et al. (1995) defined "brooding behavior" as the pattern of sitting on the eggs, and that such behavior is often associated with thermoregulatory incubation. However, such a definition of brooding behavior is considered by some authors to be problematic; for instance, Deeming (2002a) doubted the viability of such a type of incubation in oviraptors, noting that the eggs in the lower layer(s) (actually the inner ring(s)) of the clutch would not have had proper contact with the brooding adult and thus would not have benefited from the parent's body heat. In addition, behavior observed in extant non-avian archosaurs such as crocodilians could possibly provide an alternative explanation in that the parent/adult oviraptorid might have been sitting or lying atop its clutch mainly to protect it (Ferguson, 1985; Webb & Cooperpreston, 1989). A brooding bird arranges its eggs randomly in a single layer to place all the eggs below its brood patch, ensuring efficient heat transfer to all eggs, and periodically manipulates them in order to equably distribute the heat. However, the multiple-ring clutch arrangement of oviraptorids shown in previous studies (previously referred as superposed layers (Clark et al., 1999; Grellet-Tinner et al., 2006)and a pair of eggs preserved in the pelvic region of an oviraptorosaur specimen (Sato et al., 2005) imply that the clutch retained the arrangement of the eggs as they were laid. This appears inconsistent with egg manipulation during avian brooding (Varricchio et al., 1997; Varricchio & Jackson, 2016).

Some studies had offered different perspectives on the sitting oviraptors. Martin & Simmons (1995) and Carpenter (1999b) suggested that oviraptorids sat in the center of their semi-exposed egg rings: in other words, they built partially open nests. They also proposed that the oviraptors were sitting on their clutches to protect them from predators. Their suggestions were challenged by Paul (2002), who argued that it was safer to bury the eggs deep in sediments instead of exposing them to the air. However, the partially open nest structure seems to echo Deeming's view that it is unlikely for the parent to sit on the exposed blunt ends of eggs (Deeming, 2002a). It should also be noted that most extant birds construct their nests to be fully open and exposed, which allows the eggs to be manipulated to effectively allow body heat to transfer to the eggs. In addition, the eggs of extant birds are arranged in a single layer to efficiently transfer body heat from the brooding parent to all the eggs, unlike the multi-ringed clutch of oviraptors, arranged around a higher and vacant center.

All above arguments are closely related to the clutch architecture of an oviraptorid clutch, which was never rigorously investigated and detailed discussed. Thus, we would like to present a short review that presents different hypotheses regarding the architecture of an oviraptorid clutch for highlighting the aims of this study.

5-1-2 Architecture of an Oviraptorid Clutch

In the beginning, it is crucial to distinguish between a clutch, a cluster, and a nest. A clutch refers to all the eggs laid by an or several archosaur (monogamous or polygamous), at a single time or in a single reproductive season, particularly in a nest (Lack, 1948). In fossils, it is sometimes difficult to determine if all the eggs found in close proximity of each other were laid at the same time or within the same reproductive season; hence, the term "cluster" is used to describe an accumulation of eggs found in close proximity but which cannot be assigned to a single clutch with certainty (Vila et al., 2010). Werner & Griebeler (2013) and Ruxton, Birchard & Deeming (2014) concurred Vila et al. (2010)'s implication by hypothesizing that sauropods split their egg production across a number of different "clutches" since a sauropod clutch is radically smaller than their allometric estimation of a sauropod's fecundity. Despite the conceptual difference between a cluster and a clutch, an empirical discrimination between them in the fossil record is unlikely feasible.

In accordance with Hechenleitner, Grellet-Tinner & Fiorelli (2015), herein we define that a nest consists of a clutch and its associated shelter; however, the latter is often poorly preserved in the fossil record or destroyed during excavation. Varricchio et al. (1997) discovered a *Troodon* nest (MOR 963) compromising a 24-egg clutch within a shallow depression bordered by a distinct rim. However, no distinct sedimentological nest structures have been reported in oviraptorids.

Confusion and controversy have also surrounded oviraptorid clutch architecture since Sabath (1991) proposed the first taphonomic scenario to describe how the oviraptorid clutch architecture changed during fossilization. Sabath (1991) noticed that the elongate ornamented egg (=oviraptorid) clutch he investigated was prepared upside down, but failed to identify the multi-ringed and paired arrangement of the eggs (fig. 5 of Sabath, 1991). He vaguely implied that the dipping angle of the eggs decreased because of sediment compaction and suggested that the eggs in a clutch were arranged spirally. Four years later, Norell et al. (1995) proposed another interpretation of clutch architecture, in a sketch showing a *Citipati* individual sitting on a randomly arranged egg clutch (fig. 2 of Norell et al., 1995). In this sketch, the authors also implied that the eggs were laid in a pit. Dong & Currie (1996) corrected some flaws in Norell et al. (1995) reconstruction based on the oviraptorid clutch IGM 100/1008 (fig. 3 of Dong & Currie, 1996). The sketch of the IGM 100/1008 specimen showed a highly organized and paired egg arrangement with the blunt ends of the eggs pointing to a center devoid of eggs. However, it was left open whether the eggs were buried or exposed to the air. Dong & Currie (1996) also proposed that an oviraptorid nest should be reconstructed as a mound rather than as a pit as described in Norell et al. (1995), since they observed that the eggs are inclined to the ground at gentle angles (13-16 degrees) and slope away from the clutch center. However, the compaction during fossilization was not mentioned in these studies (Osborn, 1924; Norell et al., 1995; Dong & Currie, 1996; Clark et al., 1999; Fanti, Currie & Badamgarav, 2012; Norell et al., 2018). Deeming (2002a) missed the paired arrangement and blunt ends pointing to the center in his sketch (fig. 1-2 of Deeming, 2002a). To conclude, the oviraptorid clutch architecture has been interpreted several times but none of them appeared comprehensive as discussed above (Norell et al., 1995; Dong & Currie, 1996). Although the highly organized, paired arrangement of the eggs in an oviraptorid clutch has been documented (Norell et al., 1995; Deeming, 2002a; Norell et al., 2018), it was still contentious whether the eggs in an oviraptorid clutch were arranged spirally, as suggested by Sabath (1991) and Jones et al. (2012). However, several studies suggested that the eggs were arranged in superimposed circles, namely several concentric rings (Osborn, 1924; Norell et al., 1995; Dong & Currie, 1996; Clark et al., 1999; Fanti, Currie & Badamgarav, 2012; Norell et al., 2018).

Oviraptorid dinosaur nests were initially considered to belong to the covered nest type based on the high water vapor conductance of the eggshell calculated from the porosity of single eggshell fragments (Mou, 1992). However, simply estimating the total water vapor conductance based on isolated fragments of eggshell is problematic because of the heterogeneous pore distribution and shell thickness variation across the whole egg. A recent sedimentological investigation by Fanti, Currie & Badamgarav (2012) of a *Nemegtomaia barsboldi* clutch associated with a skeleton indicates that the upper layer of the clutch was not buried (or was only partially buried). Fanti, Currie & Badamgarav (2012) partly echoed Wang & Jan (1963)'s speculation that the oviraptorid dinosaur laid eggs on a mound. Finally, Wiemann et al. (2015) suggested that the oviraptorid clutch was partially open to the air based on detected pigments (reddish-brown protoporphyrin and blue-green biliverdin) and heterogeneous distribution of water vapor conductance.

Although the nesting mode (covered vs. open) was elucidated by our previous study (Wiemann et al., 2017), a detailed reconstruction for the architecutre of an oviraptorid clutch requires further investigations. In this study, we attempt to re-evaluate the hypothesis of thermoregulatory contact incubation (abbreviated as TCI hereafter) behavior based on the evidence arising from our reconstruction of an oviraptorid clutch.

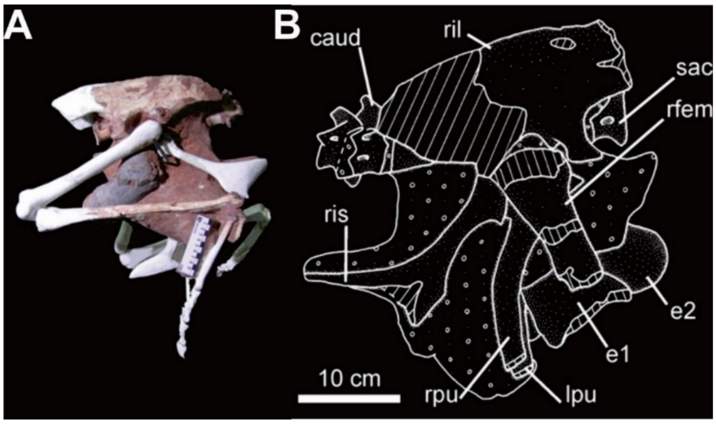

Figure 5-7 An oviraptorosaur pelvis with a pair of eggs inside reported by Sato et al. (2005). (A) A right lateral view of the specimen NMNS-VPDINO-2002-0901. (B) The osteological illustration of the specimen from left lateral view, showing the acute end of the two eggs pointing caudally.

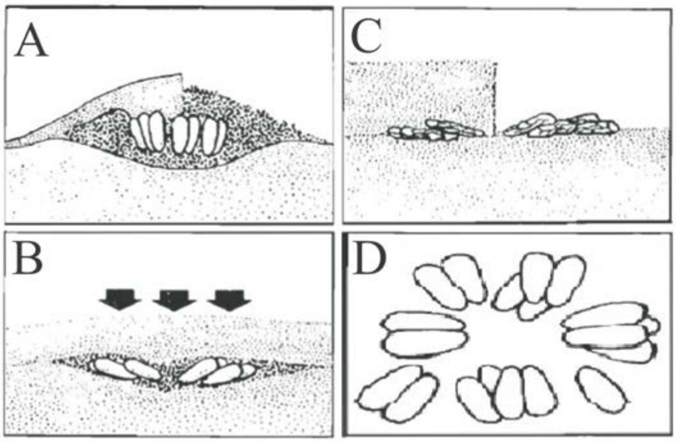

Figure 5-8 A schematic illustration of an oviraptorid egg-clutch during fossilization processes. (A) In the beginning of fossilization, the oviraptorid clutch was buried in humus and sediments. Note that the eggs were nearly vertically inclined. (B) The inclining angle of eggs increased due to the compaction through the sedimentation. (C) Finally, the eggs were crushed and nearly horizontally inclined after being compacted. (D) The top-view of the egg-clutch after compaction. Note that the acute ends point to the center in the schematic illustration. Reprinted from Sabath (1991).

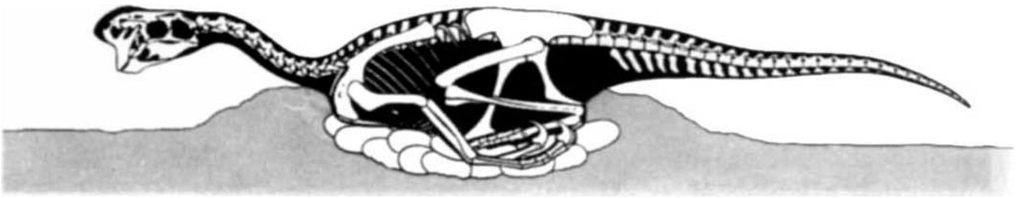

Figure 5-9 A schematic illustration of the brooding oviraptor IGM 100/979 described in Norell et al. (1995). Note that the eggs beneath the adult are randomly distributed and compacted as like modern birds. However, more reports on oviraptor egg-clutches reveal that they are actually paired arranged and highly organized. Reprinted from Norell et al. (1995).

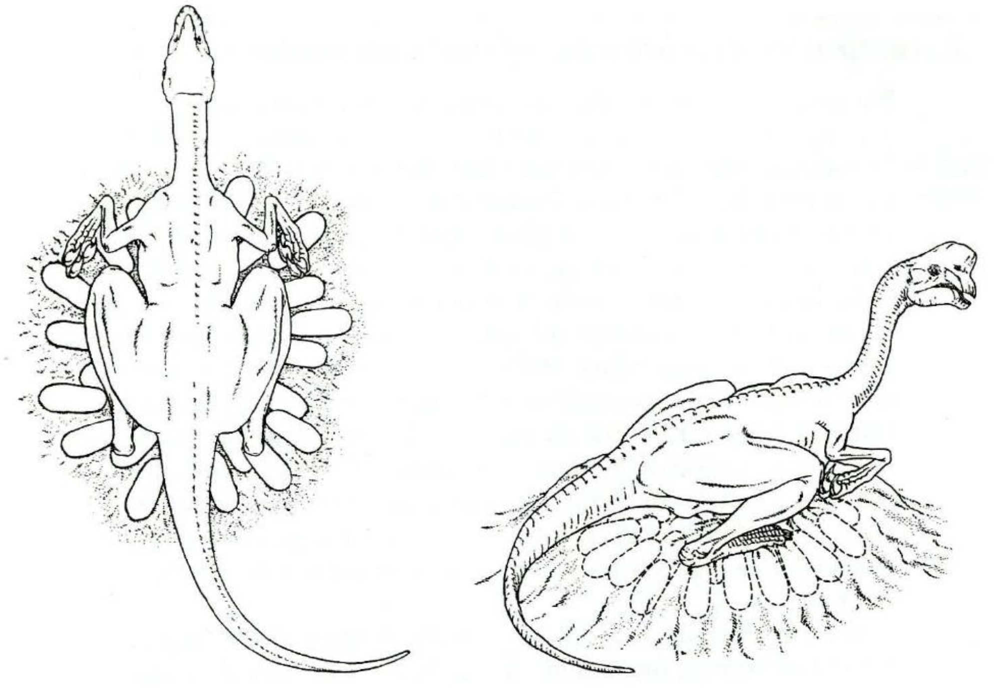

Figure 5-10 A schematic illustration of a brooding oviraptor on its clutch by Deeming (2002a). Note that the acute end of the eggs points inward to the center of the clutch as illustrated by Sabath (1991). The dashed outline of eggs refers to the buried nesting type. However, a recent study suggested that oviraptor eggs were at least partially open to the air (Wiemann et al., 2015; Yang et al., 2015).

5-2 Geological Background

The new egg clutch specimens were discovered from the Nanxiong Formation (Nanxiong Group) of the Ganzhou Basin in South China. Regional tectonics during Late Cretaceous-Early Paleogene resulted in a series of NE-SW trending extensional basins sharing similar sedimentological and stratigraphic features in southern Jiangxi and northern Guangdong, including Hongcheng Basin, Ganzhou Basin, Nanxiong Basin, etc (Bureau of Geology and Mineral Resources of Jiangxi Province, 1984). These basins are elongate and composed of red fluvial-lacustrine clastic sequences, featured by the dinosaur-containing Late Cretaceous Nanxiong Formation (Dafeng, Zhutian, Zhenshui, and Pingling Formations) and the mammal-bearing Loufuzai Group (Shanghu and Nongshan Formations).

The Nanxiong Formation in the Ganzhou Basin is composed of brownish red, medium-grained sandstone and sparsely interbedded clay sediments, dated from 66 to 72 Mya (latest Maastrichtian, Upper Cretaceous, Bureau of Geology and Mineral Resources of Jiangxi Province, 1984). Petrographic observation on sediments of the Late Cretaceous Nanxiong Formation indicates an arid to semi-arid climate in southern China during latest Maastrichtian period (Wang et al., 2015). He, Huang & Li (2017) suggested that the dinosaur egg-bearing Nanxiong Formation in the Ganzhou Basin formed in a middle to distal region of an alluvial fan based on the gravel and planar cross beds. All dinosaur egg clutches or skeleton are well-preserved, indicating that the fossils in the Ganzhou Basin were not, or only shortly, transported by the water currents.

The Nanxiong Formation yields a great number of oviraptorid dinosaurs, including *Heyuannia huangi* (Lü, 2002), *Shixinggia oblita* (Lü & Zhang, 2005), *Banji long* (Xu & Han, 2010), *Ganzhousaurus nankangensis* (Wang et al., 2013b), *Nankangia jiangxiensis* (Lü et al., 2013b), *Jiangxisaurus ganzhouensis* (Wei et al., 2013), *Huanansaurus ganzhouensis* (Lü et al., 2015), *Tongtianlong limosus* (Lü et al., 2016), and *Corythoraptor jacobsi* (Lü et al., 2017). Besides, five embryo-containing eggs (Cheng et al., 2008; Wang et al., 2016) and the oviraptorid pelvis with a pair of eggs (Sato et al., 2005) were also discovered in the same group.

5-3 Material and Methods

We re-examined specimen IVPP V9608 (Figure 5-3; Dong & Currie, 1996) and compared it with IGM 100/979 (Figure 5-2; Norell et al., 1995) . As noted, IVPP V9608 was discovered from the Djadokhta Formation in Bayan Mandahu, Inner Mongolia, China (Dong & Currie, 1996). It can be divided into two parts: a partial skeleton and an uncompleted clutch of six eggs. The partial skeleton is composed of vertebrae, the pectoral girdle, the right forelimb, and the right hind limb. Before preparation, Dong & Currie (1996) observed that the oviraptorid skeleton was lying atop the clutch. We also recorded the clutch sizes of other "brooding" specimens reported in previous studies (Table 5-1; Osborn, 1924; Norell et al., 1995; Dong & Currie, 1996; Clark et al., 1999; Fanti, Currie & Badamgarav, 2012; Norell et al., 2018).

Five remarkable complete clutches from the comprehensive collections housed at DM (2014-P0154), HGM (41H-V0074) and PFMM (0014002972, 0014003019, 0010404392) are included in this study for comparison with the clutches associated with "brooding" adults (Figure 5-2 & Figure 5-3). All of the five clutches were collected from the Upper Cretaceous Nanxiong Formation of Hongcheng Basin near the city of Ganzhou, in the southern Jiangxi Province, China, the same locality where the gravid oviraptorosaur was discovered and reported in 2005 (Sato et al., 2005). The DM and PFMM specimens were prepared by technicians of PFMM and Dr. Y.-N. Cheng of the NMNS, and the HGM specimen was prepared by technicians of the HGM (Figure 5-11; Table 5-2). All clutches were prepared from the field top as they were found in the field; however, no sedimentological evidence is available for direct interpretation of clutch architecture. The five clutches were chosen because the eggs in these clutches are well preserved and only slightly compacted. The nearly round egg cross sections indicate that these clutches still retain their original shape and arrangement (Figure 5-11) and were not affected much by sediment compaction which would have altered their cross section to an elliptical shape.

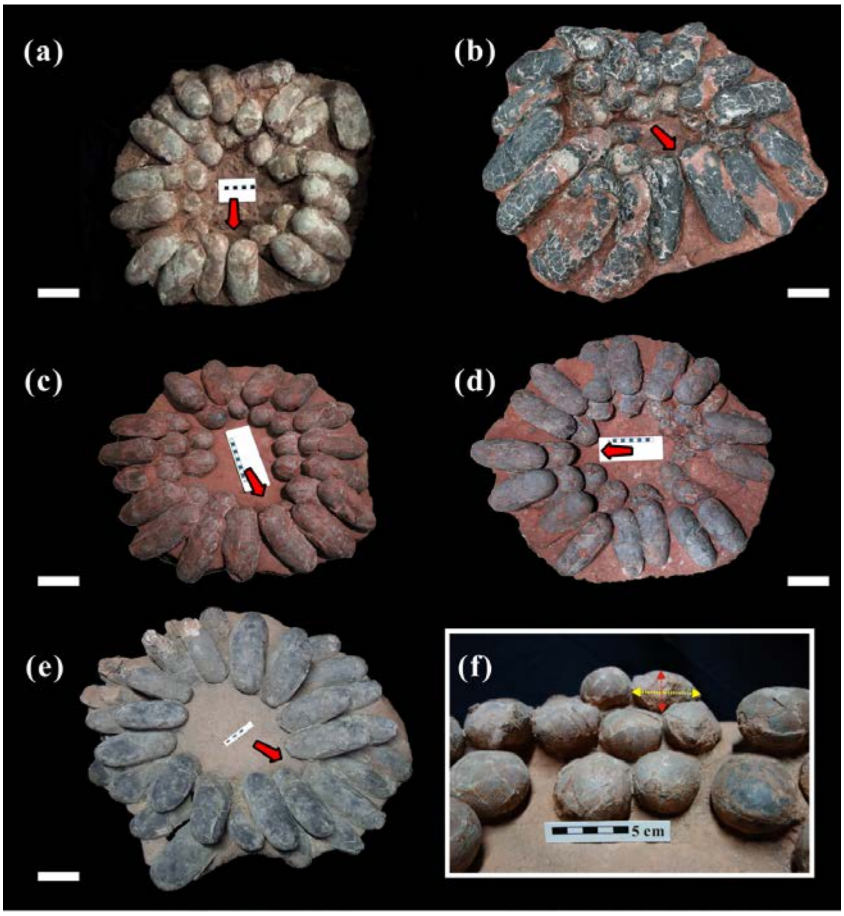

Figure 5-11 The complete oviraptorid clutches used in this study. All eggs are arranged in pairs with their blunt ends pointing towards the clutch center devoid of eggs. (A) Top view of specimen HGM-41H-V0074, a complete oviraptorid clutch with 30 eggs arranged in three superimposed rings. Two isolated eggs in the upper right might be pushed away from the uppermost ring before the burial. The vacant center is 266 mm by 213 mm. (B) Top view of specimen DM-2014-P0154, a complete oviraptorid clutch with 31 eggs arranged in four superimposed rings. The odd egg number might result from insufficient calcium supply to the female. The vacant center is comparatively smaller than in the other specimens studied, measuring only 133 mm by105 mm. (C) Top view of specimen PFMM-0014002972, a complete oviraptorid clutch with 32 eggs arranged in three superimposed rings. The vacant center is 240 cm by 135 mm. (D) Top view of specimen PFMM-0014004392, a complete oviraptorid clutch with 32 eggs arranged in three superimposed rings. The vacant center is 200 mm by 186 mm. (E) Bottom view of specimen PFMM-0014003019, a complete oviraptorid clutch with 35 eggs arranged in three superimposed rings. The vacant center is 293 mm by 280 mm, which is the largest opening among the specimens described in this study. (F) Detail of the lateral view from the center of the PFMM-0014002972 specimen. Three rings of eggs are separated by thin layers of sediments. The longer axis (46 mm) is represented by a yellow dashed line, while the shorter axis (24 mm) is represented by the red dashed line. Red arrows in (A)-(E) point to the opening in the lowermost ring. Scale bars of (A)-(E): 10 cm.

Table 5-2 Specimen number, clutch size, size of the vacant center, number of rings, locality and repository information, and stratigraphic horizon of the complete clutches described in this study. I: innermost ring; II: second ring.

Catalogue number	Clutch size	Ring No.	Size of vacant center (cm by cm)	Number of rings	Locality	Repository	Stratigraphic horizon	Prepared by
HGM-41H-V0074	30	I	26.6 by 21.3	3	Ganzhou, Jiangxi, China	HGM	Nanxiong Formation	Technicians of HGM
		II	39 by 32.5					
DM-2014-P0154	31	I	13.3 by 10.5	4		DM		Dr. Yen-Nien Cheng of NMNS
		II	27.5 by 20					
PFMM-0014002972	32	I	24 by 13.5	3		PFMM		Technicians of PFMM
		II	32.5 by 27.5					
PFMM-0014004392	32	I	20 by 18.6	3		PFMM		Technicians of PFMM
		II	30.5 by 30					
PFMM-0014003019	35	I	39.3 by 28	3		PFMM		Technicians of PFMM
		II	35 by 32.5					

To reconstruct the original nesting structure, and potential diagenetic displacement of clutches, we studied the spatial arrangement of the clutches (both with and without associated skeletons) in detail, taking sediment compaction into account. Oviraptorid eggs are generally elongated, with the ratio of long axis to girth exceeding 2.0. Based on the principles of egg formation (Romanoff & Romanoff, 1949) and supported by a pair of eggs preserved inside the pelvis of an oviraptorosaur which shows circular cross sections perpendicular to egg long axis (Sato et al., 2005), it is reasonable to assume that the original cross section of the eggs in the clutches was also circular. If we find this circular cross section to have been changed to an ellipse, we have to infer sediment compaction during fossilization as the cause (Sabath, 1991). Hence, based on the photo taken along the egg inclination from the center of each clutch (the polar view from the blunt end of an egg), we are able to estimate the amount of deformation by examining the shape of egg cross sections (Figure 5-11F & Figure **5-12**).

The factor of compaction is deduced by dividing the difference between the length of the major axis of the egg ellipse and the length of the minor axis (as viewed from the blunt end of the egg) by the restored egg diameter (Figure 5-11F & Figure **5-12**).

$$\text{Factor of compaction} = \frac{(Length\ of\ major\ axis\ of\ egg\ ellipse - Length\ of\ minor\ axis\ of\ egg\ ellipse)}{(Sum\ of\ legnths\ of\ major\ and\ minor\ axes)/2} \qquad (1)$$

Thus, we are able to reconstruct the original inclination of an egg by multiplying the measured angle of inclination with the factor of compaction (Figure 5-12; Sabath, 1991). Combined with the measured angle of inclination for the eggs in the different rings, we used the factor of compaction to geometrically reconstruct the original angle of inclination of the long axis of the eggs towards the center of the clutch (Figure 5-12; Sabath, 1991). Furthermore, to elucidate the clutch architecture, we measured the long axis and short axis of the egg rings (Table 5-2). Since the outermost ring of the studied clutches is not a complete circle, we measured only the ring size of the innermost ring (I) and second ring (II) (Table 5-2).

To access the developmental stage of the eggs of the sitting specimens, we sampled the eggshell from the IVPP V9608 specimen in order to produce a petrographic thin section with Isomet 4000 at the Steinmann Institute of University of Bonn. The eggshell thin sections were examined with a Leica DMLP Polarizing Microscope. Polarized light images were acquired with a Leica DFC420 camera by using the Leica ImageAccess EasyLab 7 software. The calcium of the eggshell is a predominant resource for eggshell formation so that the eggshell is absorbed from the innermost eggshell during embryogenesis, which provides information on the developmental stage of the eggs (Cheng et al., 2008; Weishampel et al., 2008; Wang et al., 2016).

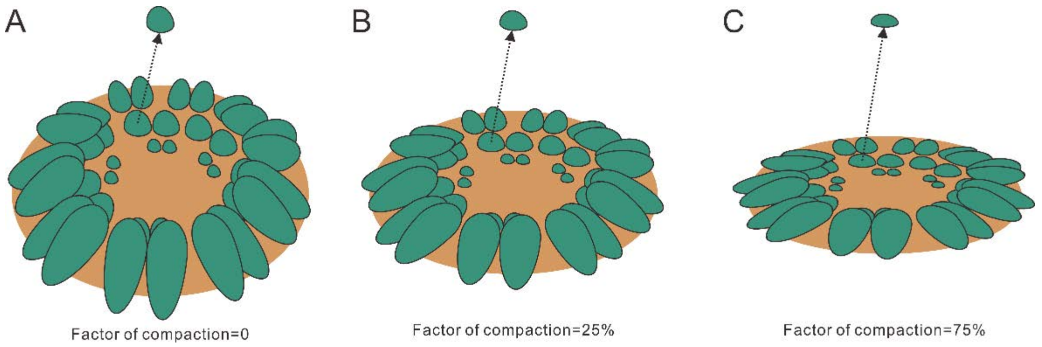

Figure 5-12 A schematic illustration of an oviraptorid clutch under different levels of compaction. (A) Original configuration of an oviraptorid clutch. (B) The configuration of an oviraptorid clutch by a compaction factor of 25%. (C) The configuration of an oviraptorid clutch by a compaction factor of 50%. Note that the change of inclining angle and shape of the eggs.

5-4 Results

Based on the surficial ornamentation of eggshells sampled from each clutch and microstructural characters (Zhao, 1975), we assigned all eggs to *Macroolithus yaotunensis*, which is laid by *Heyuannia huangi* (Cheng et al., 2008). The *H. huangi* eggs are characterized by a two-layered eggshell, an undulating boundary separating mammillary and prismatic layers, and lineartuberculate surficial ornamentation (Zhao, 1975).

In the new *H. huangi* clutches, clutch size varies from 30 to 35 eggs, which are arranged in three superimposed rings (Figure 5-11A-E; Table 5-2). None of the eggs in any of the complete clutches was hatched as evidenced by the lack of a hatching window. The clutch size of *H. huangi* clutches is significantly greater than that of the adult-associated clutches assignable to *Oviraptor philoceratops*, *Citipati osmolskae*, *cf. Machairasaurus*, *Nemegtomaia barsboldi* (Table 5-1 & Table 5-2; Osborn, 1924; Norell et al., 1995; Dong & Currie, 1996; Clark et al., 1999; Fanti, Currie & Badamgarav, 2012; Norell et al., 2018).

The eggs in a clutch were arranged in pairs with their blunt ends pointing to the center devoid of eggs, and stacked in two to four concentric, nearly circular to elliptic rings with sediment in between (Figure 5-11F). Since the vacant center are an ellipse rather than a perfect circle, we express the size of the vacant center by using the short and long axes that fit the proximal and distal points of the eggs. The lowermost, or innermost, ring has the smallest diameter and the lowest number of eggs, and both parameters increase towards the top of the clutch. Twenty-eight eggs are visible in specimen HGM-41H-V0074; however, two eggs in the innermost ring were left unexposed in order to not remove the eggs of the second ring. Two eggs are slightly offset from the rings, but still overlap with eggs of the second ring (Figure 5-11A). The innermost ring contains twelve eggs and covers an area of 26.6 cm by 20.0 cm, while the second ring has 16 eggs and covers 39.0 cm by 32.5 cm (Table 5-2). The inclination angle of the eggs ranges approximately from 27° to 33° (Table 5-2).

Specimen DM-2014-P0154 has the smallest ring size among the studied egg clutches (Figure 5-11B; Table 5-2). The innermost ring has eight eggs and covers an area of 13.3 cm by 10.5 cm, and the second ring sizes to 27.5 cm by 20.0 cm with 13 eggs (Figure 5-11B; Table 5-2). Both the third (four eggs) and fourth rings (six eggs) do not form a complete ring, being restricted to one side of the clutch; hence, no ring size can be measured (Figure 5-11B). The ratio of the area of the second ring to that of the innermost ring is 3.93, which is higher than in all the other clutches. Specimen DM-2014-P0154 also has the highest inclination angle among the studied clutches, ranging from 35° to 40° (Figure 5-11B). The egg inclination angle in specimen DM-2014-P0154 might be close to the original angle since the egg shape, when viewed from the blunt pole, is nearly circular (Figure 5-11B).

Specimen PFMM-0014002972 has 32 eggs arranged in three rings (Figure 5-11C; Table 5-2). The innermost ring (ten eggs) and second ring (16 eggs) cover an area of 24 cm by 13.5 cm and 32.5 cm by 30 cm, respectively (Figure 5-11C; Table 5-2). The inclination angle of the eggs ranges from 25° to 30°. We also measured the long and short axes of the egg cross section from the view of the blunt pole, which are 4.6 and 2.4 cm, respectively. The factor of compaction is hence 31.4%. It is estimated that the original diameter would have been around 3.5 cm. Hence, the original inclination angle would have been approximately 37° to 44°.

Specimen PFMM-0014004392 has 32 eggs; ten eggs in the innermost ring and 18 eggs in the second ring. The third ring is composed of two separate pairs of eggs (Figure 5-11D; Table 5-2). The ring size varies from 20 cm by 18.6 cm in the innermost ring to 30.5 cm by 30.0 cm in the second ring (Figure 5-11D; Table 5-2). The maximum distance between two pairs of eggs of the outermost ring is 39.0 cm (Figure 5-11D). The measured inclination angle of the eggs ranges from 28° to 35°.

Specimen PFMM-0014003019 was prepared from field bottom. It has 35 eggs arranged in three rings (Figure 5-11E). The innermost ring has five pairs of eggs with a size of 29.3 cm by 28.0 cm, and the second ring has nine pairs with a size of 35.0 cm by 32.5 cm (Table 5-2). The third ring has seven eggs distributed predominantly at the upper left side (Figure 5-11E). The measured inclination angle of the eggs ranges from 30°~34°.

To conclude, the innermost ring size of the five complete clutches ranges from 13.3 cm by 10.5 cm to 29.3 cm by 28 cm, and the second ring ranges from 27.5 cm by 20.0 cm to 35.0 cm by 32.5 cm (Table 5-2). The eggs of a clutch have similar inclination angles towards the center of the clutch (Figure 5-11). The average measured inclination angle is 30°~35° from the horizontal. The vertical distance between the highest and lowest ring ranges from eight to ten cm (Figure 5-11F). The lower egg ring in all of the complete clutches in this study has a gap devoid of eggs (Figure 5-11A-E). Some gaps are wider than the width of a pair of eggs; for instance, the gap in HGM-41H-V0074 is around eleven cm and could have accommodated another pair of eggs (Figure 5-11A). However, the gaps in the other specimens are smaller than the width of a pair of eggs (Figure 5-11B-E).

5-5 Discussion

5-5-1 Clutch Size

The clutch size of oviraptorids was poorly documented regardless of abundant discoveries of oviraptorid clutches. The adult-associated clutches, which were discovered from the Gobi Desert, yield various numbers of clutch size spanning from 6 to 22 (Osborn, 1924; Norell et al., 1995; Dong & Currie, 1996; Clark et al., 1999; Fanti, Currie & Badamgarav, 2012; Norell et al., 2018), or even an estimation of 30 (Varricchio et al., 2008). The new *H. huangi* clutches from southern China described in this study, however, have a clutch size beyond 30, significantly larger than the adult-associated clutches. The difference in clutch size between the adult-associated and new *H. huangi* clutches is basically because: 1) clutch size decreases with body size, 2) clutch size increase with latitudes, 3) the clutches from the Gobi Desert were not completed, or 4) they were simply laid by different species. However, *O. philoceratops* from the Gobi Desert and *H. huangi* from South China have a similar estimated body mass (39 vs. 42.4 kg, see the supplement of Varricchio et al., 2008 and Lü, 2002) but differ significantly in clutch size (6 vs. 30-35, see Dong and Currie and Table 2), thus precluding the first and second hypothesis. The third hypothesis was briefly mentioned by Dong & Currie (1996), though was not further discussed later. The significantly smaller clutch size of the adult-associated clutches also leads to the suggestion that the clutch-associated adults were in the period of, or short after, an oviposition. However, the third hypothesis is only persuasive if the interspecific variation (the fourth hypothesis) in clutch size is precluded, which is not feasible at the current stage. Therefore, in the later discussion, we will put emphasis on the evidence arising from the new *H. huangi* clutches and their implication for oviraptorid nesting biology.

5-5-2 Pairing, Highly-Organized Clutch Arrangement of Oviraptorids

One of the very first studies of oviraptorid clutches suggested a spirally arranged arrangement of oviraptorid clutches (Sabath, 1991). However, the highly organized, paired arrangement shows that the eggs in an *H. huangi* clutch do not interlace and thus precludes the possibility of a spirally arranged clutch. The paired arrangement in oviraptor clutches implies monoautochronic ovulation, which means oviraptors had two functional oviducts, each producing one egg per oviposition. Monoautochronic ovulation was first proposed by Varricchio et al. (1997) and was supported by (Sato et al., 2005). Grellet-Tinner et al. (2006) doubted that the pairing in *Troodon* clutches is significant, and this question also applies to oviraptor clutches. However, the paired arrangement is unequivocal both from the top view and from the bottom view (Figure 5-11). Based on retention of the original paired arrangement, it was suggested that oviraptorid eggs had no chalazae since they were not manipulated after being laid, similar to *Troodon* eggs (Varricchio & Jackson, 2003; Varricchio & Jackson, 2016). An air cell presumably was not present in an oviraptorid egg, either, because the erosion on the innermost layer of the eggshell was approximately equal in different parts of an embryo-containing egg (Yang, Cheng & Yang, 2011; Yang et al., 2015).

As pointed out by Varricchio & Jackson (2016) and Zelenitsky (2006), *Troodon* clutches show a highly-organized arrangement which is comparable to that of an oviraptorid clutch. The highly-organized arrangement is not observable in extant avian clutches, which implies that the nesting strategy of oviraptorid dinosaurs was unique. A review by Varricchio & Jackson (2016) proposed five stages in the evolution of reproduction from basal theropods to neornithines, namely (1) pre-maniraptoran theropods, (2) oviraptor-grade maniraptorans, (3) troodontid-grade paravians, (4) Enantiornithes, and (5) basal Neornithes. The highly-organized and paired arrangement are only present in the oviraptor-grade maniraptorans and troodontid-grade paravians. It should be noted that the troodontid eggs are nearly vertically arranged, which is much steeper than the 35° to 40° of oviraptorid eggs. This difference in the inclination angle makes oviraptorid reproduction even more peculiar.

Notable, some seemingly complete oviraptorid clutches have an odd number of eggs in the clutch, for instance specimen DM-2014-P0154 (Figure 5-11B). Assuming dual oviducts, an oviraptorid clutch should always comprise an even number of eggs. The first possible explanation is that an oviraptorid dinosaur might lay only one egg because of insufficient calcium supply. Second, it is also possible that the oviraptorid dinosaur pushed some eggs out of the nest in order to save the remaining eggs from predators, as ostriches do (Bertram, 1992a). Specimen HGM-41H-V0074 supports the second hypothesis, since two eggs are notably further away from the clutch center than the remaining eggs (Figure 4A).

The gap devoid of eggs can be explained by two hypotheses: (1) The gap is the female's exit after completion of oviposition; (2) the gap is simply a larger space between two pairs of eggs. Sato et al. (2005) suggested that the females came to the centers of the nests to lay neat, multilayered, ring-shaped clutches. Hence, oviraptorid dinosaurs should be similar to those of ostriches or chickens, which leave the nest after each oviposition. The highly organized clutch shows no trace of manipulation. To leave the nest without destroying the highly organized clutch, the female might have to leave a gap as an exit. The "exit" hypothesis is to be tested since no tracks were discovered in the studied clutches. However, based on the reconstruction of *Heyuannia huangi*, the mother of *Macroolithus* eggs in our studied clutches, the female should have been able to leave the clutch with one step. Besides, our measurement shows that most of the gaps cannot accommodate another pair of eggs, making the second hypothesis more feasible.

5-5-3 A Mound Nest Architecture

As reviewed above, previous studies had suggested that the oviraptorid dinosaur laid eggs in a pit (Norell et al., 1995), on an open mound (Dong & Currie, 1996), in a covered mound (Deeming, 2002a; Deeming, 2006), or in a partially open mound (Martin

& Simmons, 1995; Carpenter, 1999b; Fanti, Currie & Badamgarav, 2012). However, none of these reconstructions included all available evidence and observations. Our estimation of the inclination of eggs in an oviraptorid clutch of 35° to 40° supports the idea that oviraptors built a nesting mound. Porosity distribution suggests a partially open nest, supported by the presence of shell pigmentation, with the blunt ends end of the eggs exposed to the air.

Combining these facts, including the nest type, shell porosity data, shell pigmentation, and geometry of an oviraptorid clutch, we suggest that the eggs were laid leaning on the flanks around a mound. After finishing the first (or innermost) ring, the female partially covered the first ring of eggs with soil before continuing with the second ring of eggs. Finally, all blunt ends of the eggs were exposed to the air, while the acute ends were buried in soil or sediment, as suggested by shell porosity data and pigmented eggshells (Wiemann et al., 2015; Yang et al., 2015).

Mound-building in megapodes is considered as an apomorphic character since megapodes are a monophyletic group of galliform birds (Hansell, 2000). However, megapodes bury all eggs in the mound without exposing them to the air, which is different to the nest architecture we proposed for the oviraptorid dinosaurs. Among dinosaurs, only troodontid nests are analogous to oviraptorid nests in the aspects of paired arrangement and a center devoid of eggs. Low porosity and water vapor conductance values also suggest that troodontids built open or partially open nests (Varricchio et al., 2013). However, troodontid nests differ from oviraptorid nests predominantly in the much steeper inclination angle of eggs in the clutch. Although troodontid eggs share several physical features with extant avian eggs, such as an unornamented and tri-layered eggshell and an asymmetrical egg shape, both troodontid and oviraptorid nest architectures are so bizarre that no extant analogue exists.

5-5-4 A Reevaluation of Adult-Associated Oviraptor Clutches

Four hypotheses have been proposed for explaining the peculiar oviraptorid adult-associated clutch specimens: (1) egg stealing, (2) brooding/TCI, (3) protection, and (4) egg laying, as reviewed in the introduction. Although the hypothesis of brooding/TCI is now commonly accepted, criticism has been offered from the perspectives of biology and ornithology. For instance, Deeming (2002a) argued that the heat transfer from the adult to the eggs in the lower rings would have been insufficient for incubation. The author also pointed out that it was unlikely that the adult sat on the clutch without disturbing the arrangement of the eggs if the eggs were laid exposed on a mound. However, Deeming (2002a) did not provide an alternative hypothesis to explain the adult-associated specimens. In Norell et al. (1995)'s discussion, the term "brooding" refers only to the behavior of sitting on nests. They mentioned pythons as an example of an extant ectodermic brooding animal to imply that brooding behavior is not necessarily related to thermoregulatory incubation. However, they also suggested that brooding behavior is associated with thermoregulatory incubation, thus obscuring the definite difference between brooding and TCI behaviors, as we clarified in the introduction. Thus, in the following discussion, we put emphasis on reevaluating the TCI hypothesis based on reviewing previous arguments and evidence arising from this study in various aspects.

Based on our re-examinations of the IVPP and IGM specimens and the comparison with complete clutches, we concur with Deeming (2002a) in that it appears unlikely that the oviraptorid skeleton-clutch associations represent TCI behavior. By definition, the act of incubation comprises an adult's behavior of sitting atop its eggs with direct body-egg contact to transfer body heat from the adult to the eggs. The multi-ring clutch prevents sufficient heat transfer to the lower rings of eggs, as already noted by Deeming (2002a). Another possibility is that the oviraptorid eggs employed convection in the albumen to enhance heat transfer, with the acute ends being insulated in sediment van Brecht et al. (2005). Nevertheless, this hypothesis is refuted by the high inclination angle of the eggs in *H. huangi* clutches. The steep angle of the eggs arranged in the nest also makes it unlikely that the parent sat atop to incubate them. This is because the contact surface between any one egg in the clutch and the warm parent body might have been rather small and insufficient for incubation by body heat. A multidimensional heat transfer model also showed that the heat transfer is more efficient in horizontal component than in vertical component Turner (2002), which explained why birds arrange their eggs at a gentle angle to the ground, enlarging the body-egg-contact.

Another evidence that contradicts the TCI hypothesis, in the aspect of clutch arrangement, is the center devoid of eggs. Incubation behavior as a peculiar avian trait is always associated with a brood patch. The brood patch is a feather-less region in an incubating bird's belly, allowing for efficient heat transfer to the incubated eggs. The interpretation of incubating oviraptors is inconsistent with the clutch center devoid of eggs right where the brooding patch would have been. A incubating bird keeps its eggs close to its body (brooding patch) by building a nest as small as possible, allowing for efficient heat transfer and equal covering of the eggs. Hopp & Orsen (2004) suggested that the supposed incubating oviraptorids used their feathered wings to cover the whole clutch. Nevertheless, the skeletal reconstruction by Fanti, Currie & Badamgarav (2012) showed that *Nemegtomaia* could not cover the whole clutch. Our re-examination of the specimen IVPP V9608 also shows that the eggs are not completely covered by the sitting adult's forelimb.

Furthermore, in a modern avian paternal care system such as ostriches (Bertram, 1992a), the male came to start incubating after the clutch is completed and thus all eggs hatch synchronously. Therefore, if oviraptor males did incubate the clutch, as suggested by Varricchio et al. (2008), all eggs would have hatched synchronously. Thus, the hatching asynchrony in oviraptors suggested by Weishampel et al. (2008) either supports or precludes the TCI hypothesis. If the hatching asynchrony in oviraptorids is a result of the initiation of TCI in the onset of clutch completion, as like in bi-parental birds, the TCI hypothesis is a reasonable implication. However, since Varricchio et al. (2008)'s surmise implied a similar mating system of oviraptors to modern paternal caring birds, the TCI in oviraptors would have begun after clutch completion, which contradicts to the observation of hatching asynchrony in oviraptors.

Isotope geochemical research potentially contributes to resolve the argument of the TCI hypothesis. Eagle et al. (2015) determined body temperature of oviraptor females during periods of ovulation based on the clumped isotope analysis of eggshells. Their result showed a significantly lower body temperature of oviraptors than of modern birds, implying that oviraptors had a thermoregulatory mode unanalogous to oviraptors. In contrast, a recent study suggested that oviraptors incubated their eggs within a 35-40 range that is similar to modern birds, thus concurring with the occurrences of adult-associated clutches (Amiot et al., 2017). However, Amiot et al. (2017)'s speculation was based on the assumption that the analyzed eggshell preserves their original in vivo oxygen isotope composition. These isotopic geochemical studies thus indicate the uncertainty in elucidating dinosaur physiology.

The body temperature of incubating females, or the incubation temperature play a critical role in archosaur embryo development. The embryos of extant incubating birds (virtually all birds except Megapodidae) show an increased developmental rate after the adult starts incubating (Chaiseha & El Halawani, 2015); embryo development is inhibited when external heat provided by incubation is lacking. However, no embryonic remains have so far been reported from the eggs of any of the adult-associated clutches (Osborn, 1924; Norell et al., 1995; Dong & Currie, 1996; Clark et al., 1999; Fanti, Currie & Badamgarav, 2012; Norell et al., 2018) despite many of the eggs reveal their inside in fractures. Furthermore, the inside of the eggshell of eggs from adult-associated clutches shows no erosion (fig. 2 of Norell et al., 1995 and Figure 5-3D), indicating that at least development of the embryos had not commenced yet at the time of death or the embryos were at an early stage of development. This contrasts with the common occurrence of *in ovo* oviraptor embryos that are not associated with adults (Norell et al., 1994; Cheng et al., 2008; Weishampel et al., 2008; Wang et al., 2016). Norell et al. (2018) re-examined the first oviraptorid adult-associated clutch (AMNH FARB 6508 and 6517, Osborn, 1924) and reported remains of a juvenile oviraptorid (AMNH FARB 33092) that are associated within the adult-associated clutch; however, it is uncertain if the juvenile oviraptorid hatched from the clutch. Eggshell sampling from the egg clutch (AMNH FARB 6508) would possibly indicate if the eggs are in the stage of hatching.

Therefore, to briefly conclude, the TCI hypothesis appears questionable based on all available evidence. If the clutch-associated adults were not incubating their clutch, their brooding (sitting) posture might correspond to protection, pre-oviposition, the process of an oviposition, or post-oviposition. Since there is no evidence of eggs inside the clutch-associated adults, it is unlikely that the clutch-associated adults were during, or before, an oviposition. In the following discussion, we would like to present the speculation on the basis of the comparison of clutch size and embryo development to support the hypothesis of egg laying.

5-5-5 Scenario of a Laying Oviraptorid

Compared to the five new *H. huangi* clutches, each of which contains more than 15 pairs of eggs arranged in multiple superimposed elliptical rings (Figure 5-11A-E), the oviraptorid adult-associated clutches appear uncompleted if these clutch-associated would have produced similar amount of eggs. If this uncompletedness is not due to incomplete recovery of the fossil (which is unlikely given the fact that in all five known "brooding" specimens the clutches are incomplete) or interspecific variation of fecundity, it would suggest that the female had not completed laying her eggs when she died. Varricchio et al. (2008) suggested that oviraptor clutches were completed by several females mating with the same male, i.e., polygamy behavior. Our study shows that an oviraptorid clutch has more than 15 pairs of eggs. Hence, it is intriguing to speculate how an oviraptorid clutch was completed by several females. Two possible modes are suggested based on the clutch arrangement. (1) The dominant female came to lay the first pair of eggs, and another female laid the second pair, and so on until there was no more space left in the first ring. Then the first ring of eggs was covered up for laying the second ring of eggs. This mode is similar to that observed in ostriches (Bertram, 1992b). (2) The first (or dominant) female came to lay and cover the first ring of eggs. Afterwards, another female came to the same nest to lay and cover the second ring of eggs, and so on. However, if we assume the laying period of an oviraptor to have been similar to that of an ostrich, which is one egg (a pair of eggs for oviraptorids) every other day, a 15-pair clutch would take "at most" 15 days to complete in mode I, but more than 30 days in mode II where only two females are involved, suggesting the first mode as the more likely one.

Finally, we offer a scenario of how oviraptorid dinosaurs laid eggs. The female chose a site and piled up a mound of soil or sediment and then sat on the center of the mound to oviposit. After laying the first ring of eggs, the female covered this layer with the blunt ends of the eggs exposed to the air, and then continued to lay the second and third ring of eggs. The adult-associated clutches represent animals that died atop their clutch, possibly while resting, before completing the clutch. Death may have been caused by a sandstorm that buried the adult and the uncompleted clutch all of a sudden.

5-5-6 Nest Architecture and Clutch Arrangement of Oviraptorosaurs

Caenagnathid and oviraptorid dinosaurs constitute the theropod clade Oviraptorosaur. The reproductive biology of oviraptorid dinosaurs were more extensively explored based on the gravid specimen, adult-associated clutches, and embryo-containing eggs (Osborn, 1924; Norell et al., 1995; Clark et al., 1999; Sato et al., 2005; Cheng et al., 2008; Weishampel et al., 2008; Fanti, Currie & Badamgarav, 2012; Wang et al., 2016; Norell et al., 2018). Recently, the Baby Louie, a large caenagnathid oviraptorosaur *Beibeilong sinensis* embryo, was described detailed and connected to *Macroelongatoolithus xixiaensis* (Pu et al., 2017). The caenagnathid clutch is also composed of two or more rings of eggs with the blunt ends pointing to the center, as their sister group oviraptorids did. Hence, it is very likely that the conclusion from this study also applies to caenagnathid clutches, which makes the peculiar clutch arrangement as an apomorphic character of oviraptorosaurs.

5-6 Conclusion

As reviewed by Varricchio & Jackson (2016), oviraptor-grade maniraptorans represent one of five evolutionary stages of reproduction from basal theropod dinosaurs to neornithines. The reproductive biology of oviraptorid dinosaurs is therefore crucial for further understanding the evolution of reproduction from dinosaurs to birds. Although there were thousands of oviraptorid clutches discovered in China and Mongolia, no studies ever completely investigated the clutch arrangement and described the configuration of an oviraptorid clutch. Our study describes oviraptorid clutch arrangement in detail, hopefully correcting previous flaws and aiding in future studies. We conclude that a complete oviraptorid nest shows the following features: (1) a mound with the slope inclination 35° to 40° on which the eggs were leaning; (2) the eggs are highly organized and arranged in pairs in three to four elliptical rings with sediments interbedded in between; (3) a center devoid of eggs and an egg number increase towards the top; (4) the eggs were pigmented and partially exposed to the air. We note that oviraptorid dinosaur clutches, or even all oviraptorosaur clutches, are so peculiar that it might represent an apomorphic nesting trait deviating greatly from the strategies characterizing the bird stem line.

Our study also deduces the extinct reproductive biology of oviraptorid dinosaurs, based on detailed inspection of previously reported adult-associated clutches and newly described *H. huangi* clutches. Our observations support the hypothesis that the clutch-associated adults were actually resting after laying instead of incubating.

Chapter 6 A new embryo-bearing clutch reveals asynchronous hatching in oviraptorid dinosaurs

PUBLICATION

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ABSTRACT

Dinosaur eggs with embryos inside have been discovered in several localities around the world and provide insights into dinosaur reproductive biology and breeding ecology. Most of the known embryo-containing eggs can be referred to oviraptorid theropods. However, most of these eggs cannot be associated with a specific clutch, and only one partial, poorly preserved embryo-bearing oviraptorid clutch has been reported, stemming from the Late Cretaceous Nemegt Formation of Mongolia. Here we report another partial, but better preserved oviraptorid clutch consisting of three embryo-containing eggs, a pair and a single one, from the Late Cretaceous Nanxiong Formation near Ganzhou in Jiangxi Province, southern China. These embryo-bearing eggs are distinct from those of the Mongolian clutch and are assigned to the oospecies *Macroolithus yaotunensis* based on the external ornamentation and internal microstructure of the eggshells. Osteological and eggshell histological analyses reveal that the two embryos in the paired eggs were closer to hatching than the one in the single egg, indicating an asynchronous hatching mode in oviraptorid dinosaurs. This new clutch, together with the Mongolian clutch, suggests that asynchronous hatching might be a general feature of oviraptorid dinosaurs and represent the earliest record of hatching asynchrony.

Furthermore, the cranial part of one of the paired embryos sits near the blunt end pointing toward where the center of the clutch would have been. This observation thus concurs with our previous reconstruction of a partially open oviraptorid clutch

(Chapter 5). The uncovered blunt end of an eggs would have been the only exit for embryo hatching. The combination of the new evidence arising from this study and previously published evidence from egg coloration, partially open clutches, polygamy behavior, communal nesting behavior, and the absence of contact incubation, we infer a peculiar, unique reproductive biology in oviraptorids. The nesting strategy of oviraptorid dinosaurs lacks a modern analogue, highlighting the limitations of the actualistic approach and the need for more rigorous analysis of all available evidence.

6-1 Introduction

6-1-1 Hatching Asynchrony in Reptiles, Birds, and Dinosaurs

Hatching asynchrony occurs in birds when incubation of the eggs commences before the whole clutch is finished (Figure 6-1). In complete synchrony, incubation begins after the clutch is finished and all eggs hatch at the same time. However, in complete asynchrony, incubation begins when the first egg is laid, and all eggs hatch gradually over a period of time. Some birds show partial synchrony (or partial asynchrony), in which incubation begins after several ovipositions. Non-avian reptile eggs hatch synchronously because they are laid *en masse* and develop simultaneously. A study discovered inter-embryo communication between siblings in the same turtle clutch, coordinating the pace of their development and then hatching together (McGlashan, Spencer & Old, 2012). This mechanism was also observed in snakes (Aubret et al., 2016). Albeit speculative, this mechanism probably also existed in those dinosaurs that laid the whole clutch simultaneously and buried their eggs without incubation and parental care, such as the basal sauropodomorph *Massospondylus* (Reisz et al., 2012), sauropods (Chiappe et al., 1998; Sander et al., 2008), hadrosaurs (Horner, 1999), and therizinosaurs (Kobayashi et al., 2013).

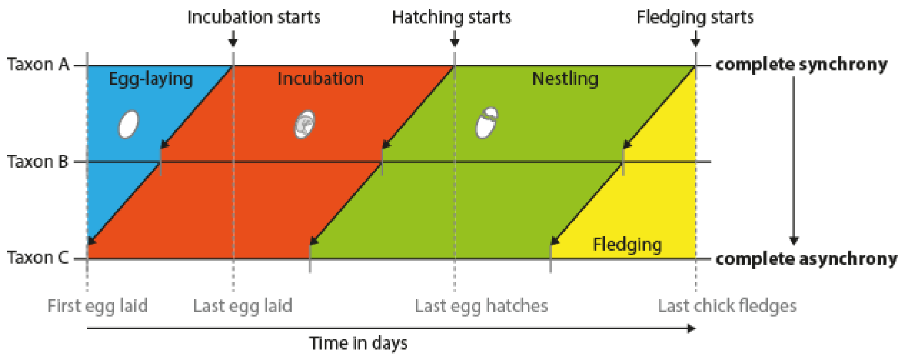


Figure 6-1 A schematic illustration of the four nest stages following the Hussell (1985) model of hatching asynchrony. In complete synchrony, incubation begins after the clutch is finished and all embryos hatch and all chicks fledge at one time. However, in complete asynchrony, incubation begins when the first egg is laid, and embryos hatch and chicks fledge gradually over a period of time. Some birds show partial synchrony (or partial asynchrony), in which incubation begins after several ovipositions and the fledging period is correspondingly intermediate. Modified from Lee & Lima (2016).

Chapter 6: Hatching Asynchrony

Among non-avian dinosaurs, titanosaurs, oviraptorosaurs, and troodontids yield the most abundant fossil record of eggs and embryos (Figure 6-2) (Norell et al., 1994; Varricchio et al., 1997; Chiappe et al., 1998; Varricchio, Jackson & Trueman, 1999; Chiappe, Salgado & Coria, 2001; Norell, Clark & Chiappe, 2001; Varricchio, Horner & Jackson, 2002; Cheng et al., 2008; Weishampel et al., 2008; Wang et al., 2016). Previous research has suggested that sauropods buried their eggs in the substrate based on shell porosity analysis of sauropod eggs from France, Spain, and India (Seymour, 1979; Sander et al., 1998; Deeming, 2006; Sander et al., 2008). Chiappe et al. (2004) studied six egg clutches from Auca Mahuevo, Argentina, and interpreted it as an open nest of a sauropod dinosaur based on the assumption of lower porosity of eggshells (Chiappe et al., 2004). Later, two studies concurred that the Auca Mahuevo titanosaur eggs were incubated in high-humidity conditions (Grellet-Tinner, Chiappe & Coria, 2004; Grellet-Tinner et al., 2006). However, Jackson et al. (2008) and Sander et al. (2008) demonstrated that the Auca Mahuevo titanosaur eggs have low porosity, thus indicating that these dinosaurs did not bury their eggs (open nesting), again echoing Chiappe et al. (2004)'s interpretation.

Hechenleitner, Grellet-Tinner & Fiorelli (2015) argued against the "open nesting hypothesis" by proposing that titanosaurs adopted mound nesting or burrow nesting. While no fossils similar to the gravid oviraptorosaur Sato et al. (2005) have been reported for sauropods, it is most likely that all sauropods deposited clutches in one event and that all eggs hatched synchronously without incubation by adults based on evidence discovered so far (Chiappe et al., 2004; Jackson et al., 2008; Sander et al., 2008; Ruxton, Birchard & Deeming, 2014).

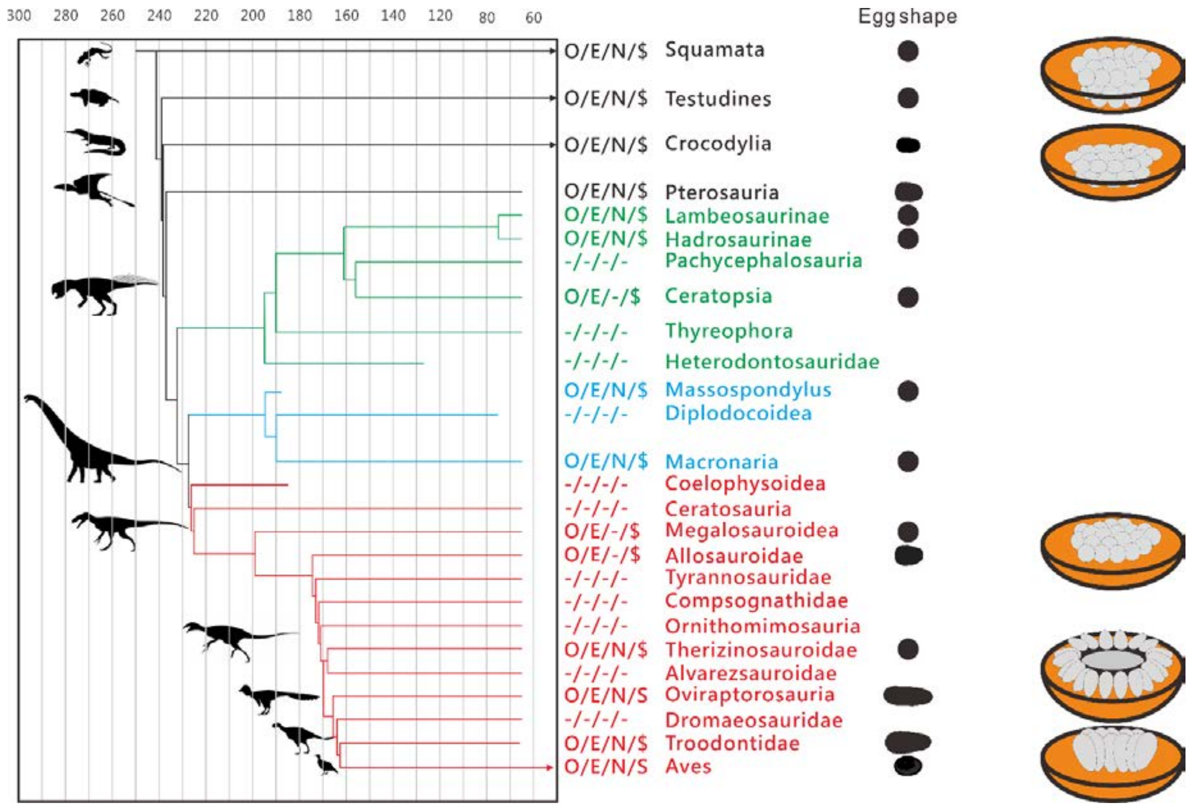


Figure 6-2 Time-calibrated cladogram of reproduction characters in diapsids (modified from Reisz et al., 2012 and Lee et al., 2014). The annotations next to the cladogram refer to the discoveries of relevant fossil evidence. Abbreviations: O, eggs; E, embryos; N, nests or clutches; S, eggshell surface ornamentation; $, no surface ornamentation on eggshell; -, no records. The nest type of turtles, crocodiles, therizinosaurs, oviraptorosaurs, and troodontids are also sketched. However, the nest types of most clades among dinosaurs are still uncertain.

Chapter 6: Hatching Asynchrony

Oviraptorid dinosaurs left behind the most abundant fossil record, providing insights into dinosaur reproduction biology, such as two gravid females (Sato et al., 2005; He et al., 2012), numerous embryo-containing eggs (Chiappe et al., 1998; Chiappe, Salgado & Coria, 2001; Norell, Clark & Chiappe, 2001; Cheng et al., 2008; Weishampel et al., 2008; Wang et al., 2016), and several clutch-adult associations (Norell et al., 1995; Dong & Currie, 1996; Clark et al., 1999; Fanti, Currie & Badamgarav, 2012; Bi & Xu, 2017; Norell et al., 2018). Most oviraptorid embryo-containing eggs were individually made available to scientists without discoveries of siblings from the same clutch. In 2008, four partial eggs with embryonic remains (two of which adhere to each other) from the Nemegt Formation at Bugin-tsav, in the southwestern Gobi Desert of Mongolia, were reported and provided insights into hatching asynchrony in oviraptorid dinosaurs (Weishampel et al., 2008). However, poor preservation precluded attribution of the four embryo-containing eggs to a single clutch. Although Weishampel et al. (2008) claimed that the four eggs were found as an aggregate of fragments in a circular depression, the interpretation that the four embryo-containing eggs were from the same clutch remained controversial because of the absence of evidence for direct associations. Although the study by Weishampel et al. (2008) improved our understanding of the reproductive biology of oviraptorid dinosaurs, the poor preservation of the material led to uncertainty about hatching asynchrony. Furthermore, the material did not provide further insights into oviraptorosaur reproductive ecology, which will be one of the major focuses in this study.

6-1-2 Identification of the Egg Producer

The assignment of dinosaur eggs to a specific dinosaur clade or species is a longstanding, vexing problem. Since the systematic naming of dinosaur eggs, that is, ootaxonomy, was established by Chinese paleontologist Zikui Zhao of the Institute of Vertebrate Paleontology and Paleoanthropology (Zhao, 1975), paleontologists have a common language for exchanging knowledge about dinosaur eggs. Parataxonomy is rooted in the identification of biomineralic patterns such as microstructures, thickness of different crystallite layers, and thickness ratio of the layers to each other. The main problem with this parataxonomy is that similar eggshell microstructures occur in different taxa. Thus, a definitive assignment of an oospecies to a biological dinosaur species is only possible based on clutch-adult associations, embryo-containing eggs, or unlaid eggs inside a female.

Dinosaur embryo fossils inside eggs are known from *Massospondylus carinatus* (Reisz et al., 2005), titanosaurs (Chiappe et al., 1998), *Hypacrosaurus stebingeri* (Erickson et al., 2017), *Protoceratops andrewsi* (Erickson et al., 2017), *Torvosaurus sp.* (Araújo et al., 2013), *Lourinhanosaurus antunesis* (Mateus et al., 1998; de Ricqlès et al., 2001), therizinosaurs (Kundrát et al., 2008), the caenagnathid *Beibeilong sinensis* (Pu et al., 2017), oviraptorids such as *Citipati osmolskae* (Norell et al., 1994) and possibly *Ingenia yanshinii* (Reisz et al., 2012) and *Heyuannia huangi* (Cheng et al., 2008), and *Troodon* (Varricchio, Horner & Jackson, 2002). Oviraptorid embryos are commonly discovered in China and Mongolia. However, incomplete preservation and immature anatomical features of embryos hamper convincing assignment (Cheng et al., 2008; Shao et al., 2014; Wang et al., 2016).

6-1-3 Embryology of Oviraptorids

Individual embryo-containing eggs discovered so far have indeed contributed to our understanding of dinosaur embryology; however, paleontologists have been unable to elucidate the entire developmental sequence of dinosaur embryos in the absence of multiple monotaxic embryos. At the Ukhaa Tolgod site of Mongolia, Norell et al. (1994) discovered a theropod embryo that displays several apomorphies of the Oviraptoridae, possibly *Oviraptor philoceratops*. Later, four oviraptorid embryos from Bugin-Tsav in ovo were reported, potentially indicating the hatching asynchrony of oviraptorids (Weishampel et al., 2008). Cheng et al. (2008) described two oviraptorid embryos (NMNS-0015276-F02-embryo-01 and CM-61) from the Nanxiong Group of Ganzhou Basin, Jiangxi Province, China and assigned them to *Heyuannia huangi* based on eggshell microstructure and geographical affinity to previously described *H. huangi*. Wang et al. (2016) reported three isolated oviraptorid embryo-containing eggs from Nankang District, Ganzhou County, Jiangxi Province, China (IVPP V20182, IVPP V20183, and IVPP V20184). Although the eggshell microstructure supports the assignment to *Heyuannia huangi* (personal communication with Zhang, Shukang), they assigned the embryos Oviraptoridae *incertae sedis* because the embryos did not show autapomorphic features. The study also described 20 osteological features that change substantially during ontogeny in oviraptorids. For instance, the distal caudal vertebrae change from unossified in the immature stage to ossified in the mature stage. Moreover, Later, the *Beibeilong sinensis*, one of the best preserved dinosaur embryos, was described, thus providing the first known association between skeletal remains and eggs of caenagnathids (Pu et al., 2017). These discoveries demonstrated the abundance of oviraptorid, or oviraptorosaurian, embryos in China and Mongolia (Norell et al., 1994; Cheng et al., 2008; Weishampel et al., 2008; Shao et al., 2014; Wang et al., 2016; Pu et al., 2017). Despite many reports of oviraptorid embryonic remains *in ovo*, the position of an oviraptorid embryo *in ovo* is unclear and poorly discussed. In Norell et al. (1994)'s report, the skull of the undisturbed embryo *in ovo* (IGM 100/971) sits near the blunt end, which is represented by the node ornamentation of the eggshell. In Pu et al. (2017), the *Beibeilong* embryo was discovered with another five eggs and the skull of the *Beibeilong* embryo points to the center of the clutch as indicated by the long axes of the other five eggs. However, the pose of an oviraptorid embryo *in ovo* was never discussed in these studies (Norell et al., 1994; Cheng et al., 2008; Weishampel et al., 2008; Shao et al., 2014; Wang et al., 2016; Pu et al., 2017).

6-1-4 Nesting Biology of Oviraptorids

A complete oviraptorid clutch consists of more than 30 eggs arranged in pairs which in turn are arranged in three to four superimposed rings (see Figure 6-3 & Chapter 5). Pairing implies monoautochronic ovulation in oviraptorid dinosaurs, which also was inferred based on an oviraptorosaurian pelvis with a pair of eggs inside (Sato et al., 2005). The paired eggs in an oviraptorosaur pelvis and paired arrangement in oviraptorid clutch preclude post-laying parental manipulation, indicating a sequential laying from inner ring to outer ring. In the clutch, the long axis of the eggs is inclined at about 60 degrees from the vertical towards the clutch center, and the blunt ends pointing towards the clutch center (see Chapter 5). These features highlighted a peculiar nesting mode of oviraptorid dinosaurs and offer crucial geopetal information for understanding the evidence and inference later.

In addition to their peculiar nesting mode, oviraptorid dinosaurs was hypothesized to exhibit some unique avian behavioral characters. Norell et al. (1995) proposed brooding behavior in oviraptorid dinosaurs based on a report of the egg clutch-adult association in the oviraptorid dinosaur *Citipati osmolskae* from Mongolia. In this report, they only proposed "sitting behavior atop a clutch" but not "contact incubation behavior." Later discoveries of oviraptorid adult-associated clutches (*Oviraptor philoceratops*, *Nemegtomaia barsboldi*, cf. *Machairasaurus* and *Citipati osmolskae*) further suggested that the behavior of sitting atop a clutch is a shared character in Oviraptoridae (Norell et al., 1995; Dong & Currie, 1996; Clark et al., 1999; Fanti, Currie & Badamgarav, 2012; Norell et al., 2018). However, more and more studies imposed the "incubation behavior" on derived feathered dinosaurs in the absence of a detailed examination of all available evidence. Yang et al. (2018b) reported five complete oviraptorid nests excavated from Jiangxi Province, China, with more than 30 eggs, and found sediment interbedded between the stacked rings of eggs. This would mean that heat was difficult to transfer to the lower part of the clutch, which suggests that the "brooding" specimens could represent guarding behavior instead of incubating as shown by some extant birds. Deeming (2002a) also pointed out that simply using the close physical association of the *Oviraptor* adult with the eggs is insufficient for inferring brooding behavior (here he obfuscated brooding and incubation). Therefore, there is no consensus on the presence and mode of putative brooding behavior in non-avian dinosaurs.

Furthermore, Varricchio et al. (2008) proposed polygamy behavior in oviraptorid dinosaurs based on their ratio of clutch volume to adult mass that closes to the one of modern polygamous birds. Polygamy behavior is contributed by paternal care and communal nesting behaviors. Whereas the hypothesis of paternal care in oviraptorids was still in debate, the communal nesting behavior in oviraptorids was later supported by elemental analyses of eggshells from the same clutch that shows inter-pair differences in phosphorus distribution, which is an indicator of female age (Yang et al., 2016). In this chapter, we only discuss the communal nesting behavior since it is pertinent to our hypothesis. We attempt to test above two hypotheses—brooding and communal nesting behaviors, based on evidence from this study and thus provide a comprehensive nesting biology model for oviraptorid dinosaurs.

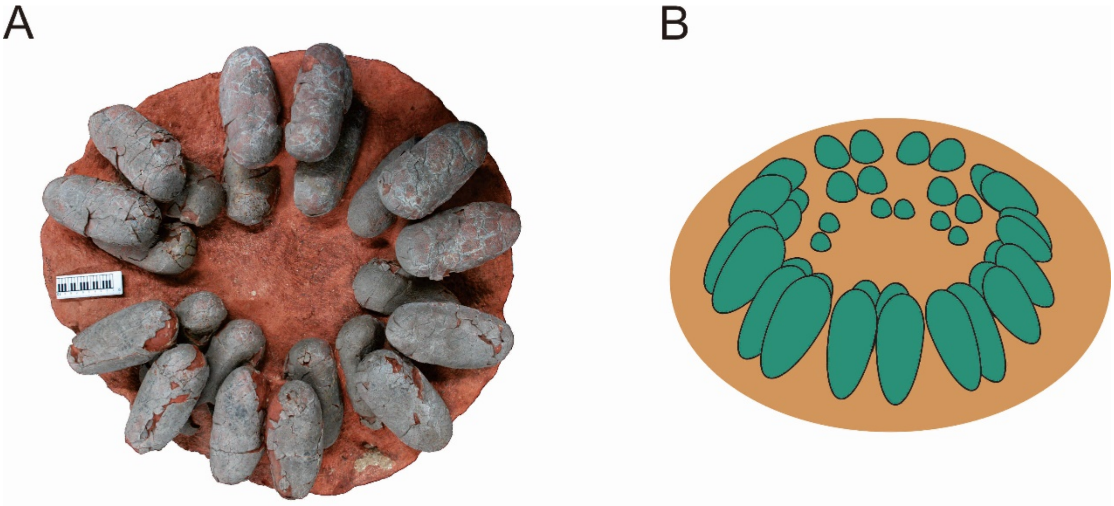


Figure 6-3 A representative oviraptorid clutch and reconstruction of the nest. (A) Top view of an oviraptorid clutch housed at the Shishang Museum of Natural History, Taiwan (SMNH-0010403018). This clutch illustrates that the eggs are arranged in pairs with their blunt ends pointing to the clutch center, as well as that the eggs are arranged in superimposed rings with sediment in between layers. This clutch preserves two superimposed rings, with 12 eggs in the outer (upper) one and 10 in the inner (lower) one. Note that the original dip of the eggs would have been much higher than what is preserved due to compaction during fossilization. (B) A semi-open nest reconstruction based on this and other well preserved oviraptorid clutches. The reconstruction shows three superimposed layers with 10 pairs of eggs in the uppermost ring, four pairs exposed in the middle rings, and three in the lower ring, visualizing that some eggs may have been completely buried by sediment at times.

6-1-5 Hatching Asynchrony: An Ecological Perspective

Asynchronous hatching in birds has long been a topic of interest to ornithologist. Several hypotheses have been proposed to explain hatching asynchrony in birds, including (1) the "brood reduction hypothesis" (Lack, 1954), (2) the "feeding constraint hypothesis" (Hussell, 1972; Hussell, 1985; Mock & Schwagmeyer, 1990), and (3) the "nest failure hypothesis" (Clark & Wilson, 1981). Among these three hypotheses, the "nest failure hypothesis" has been supported most frequently by different theoretical and empirical experiments. Were review these hypotheses in more detail below.

(a) Brood reduction hypothesis (Lack, 1947; Lack, 1954): This hypothesis noted that a significant hatching asynchrony creates clear age differences in the chicks. Hence, the first hatchling can obtain most of the reproductive investments from the parents and ensure the delivery of the parents' gene pool to the next generation.

(b) Feeding constraint hypothesis (Hussell, 1972; Hussell, 1985; Mock & Schwagmeyer, 1990): This hypothesis suggests that the hatching asynchrony serves to avoid peak energy demand. If all eggs hatch at once, the parents will suffer from fatigue due to such a high demand.

(c) Nest failure hypothesis: Clark & Wilson (1981) proposed that hatching asynchrony is a strategy to reduce total nest failure. According to this hypothesis, the ratio of daily nest mortality during the posthatching period to daily nest mortality during the prehatching periods corresponds to the degree of hatching asynchrony. That is, if offspring are at the higher risk after hatching than before hatching, then hatching synchrony is favored. Conversely, hatching asynchrony is favored if offspring are at higher risk in the egg stage than in the hatchling stage.

Since dinosaurs are the closest relatives of modern birds, paleontologists tended to apply the bird model to dinosaurs for interpreting their biology, ecology, and behaviors. For instance, Varricchio & Jackson (2016) considered oviraptorids and troodontids as an intermediate stage of reproductive biology toward modern avian mode, which was questioned by our previous study (Chapter 5). Here we attempt to test if aforementioned bird models for hatching asynchrony are applicable to dinosaurs and implicate a possible model for dinosaurs based on the evidence arising from this study.

6-2 Methods

6-2-1 Material and Geological Background

An individual egg (SMNH-20140105-1) and a pair of eggs (SMNH-20140105-2 and SMNH-20140105-3), all with embryonic remains, constitute the specimen SMNH-20140105. Hereafter, the eggs will we termed egg I (SMNH-20140105-1), egg II (SMNH-20140105-2), and egg III (SMNH-20140105-3) for ease of discussion. Egg I is from a higher ring than the pair. Based on eggshell surface ornamentation and histology

The partial clutch was discovered in the Late Cretaceous Tangbian Formation, Nanxiong Group, Ganzhou Basin, southern Jiangxi Province, China. Geographically, the discovery quarry is located in the technological development zone near Dayu County of Ganzhou City. Geologically, the Ganzhou Basin is composed of two NE-SW striking sub-basins, including the northeastern part and the southwestern part (Figure 6-4). Like most other red bed basins in Jiangxi Province, the Ganzhou Basin is a result of Mesozoic extensional tectonic activity and thus shows a "domino-style" stacking pattern. The specimen SMNH-20140105 was discovered in the southwestern part of the Ganzhou Basin that is filled with dark red purplish sandstone with interbeds of conglomerate.

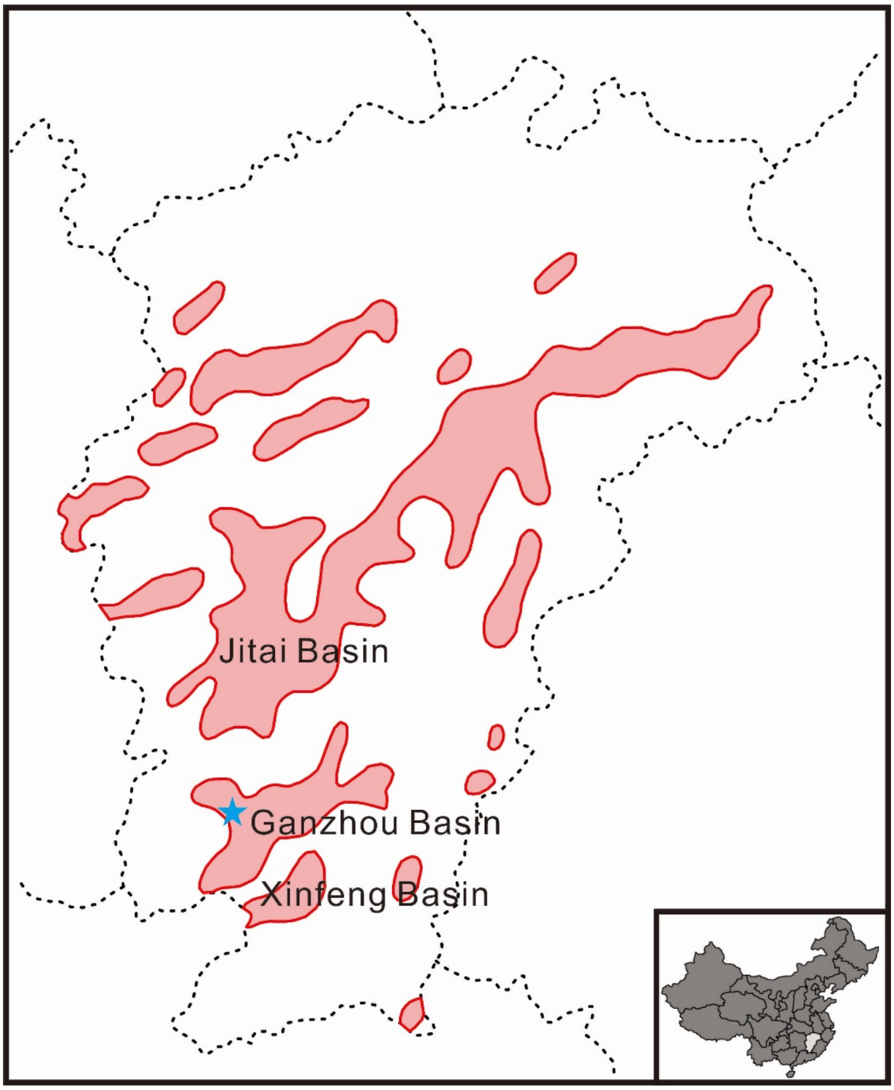


Figure 6-4 Map of Jiangxi Province, China and distribution of red bed basins. The blue star indicates the locality where the studied specimen SMNH-20140105 was discovered. Red areas are Cretaceous red bed basins.

6-2-2 Preparation and Photogrammetry

After the discovery in 2014, the specimen SMNH-20140105 was acquired by the Shishang Museum of Natural History for further preparation and studies. All three eggs were complete in the same block as shown in Figure 6-5 when collected. Meticulous preparation of each egg was only possible after separating them. The preparators at

SMNH and Tzu-Ruei Yang observed the separation and preparation. Each egg was prepared mainly from the bottom utilizing a micro-sandblaster and air scribes at the SMNH (Figure 6-5). Although the stratigraphic orientation of SMNH-20140105 was not recorded in the field, the specimen contains identifiable geopetal features that indicate the original orientation (detailed description in section 6-4-1) which is crucial for our further interpretation.

Egg I was prepared from both sides but failed to show many articulated embryonic remains (Figure 6-6; Appendix III). Egg II was prepared from the bottom only (Figure 6-7; Appendix III). To avoid destruction of the little distorted, but well-preserved top-side of egg III, mechanical preparation was only conducted from the bottom side after separating the other two eggs (Figure 6-5 & Figure 6-8; Appendix III).

For producing 3D models for each embryo-containing egg (Appendices III), digital photos were taken with a Canon EOS 550D DSLR camera and imported into Agisoft PhotoScan version 1.4.1 (www.agisoft.ru/products/photoscan/professional/). These digital photos were aligned for building a sparse point cloud. Based on the sparse point cloud, we produced a polygon mesh for a 3D model.

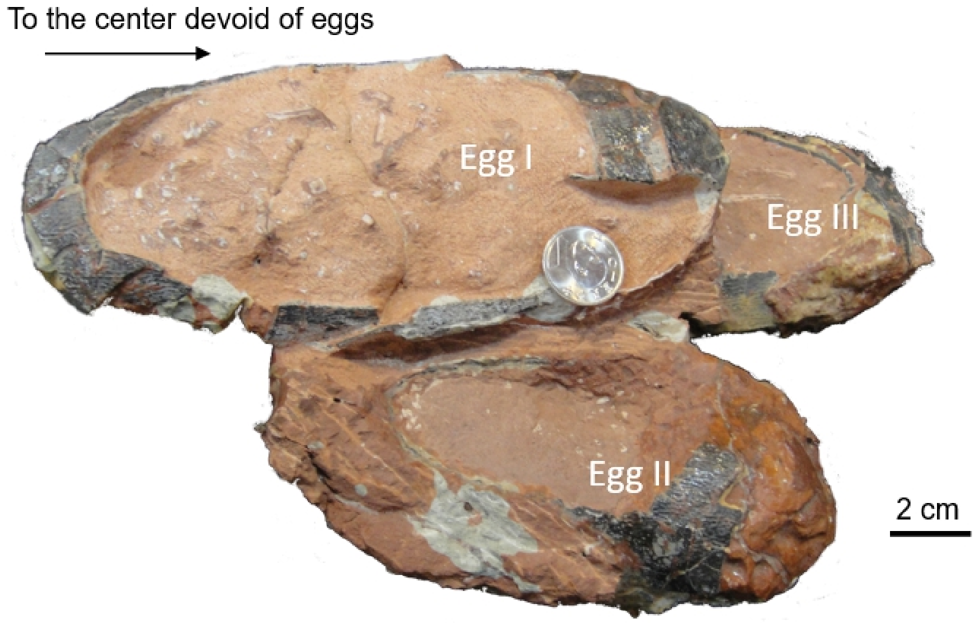


Figure 6-5 Oviraptorid eggs (SMNH-20140105) containing embryological material before preparation and separation into the individual eggs. This specimen is shown in a field-top view. The arrow points to the center of the original clutch, which can be identified based on the blunt ends of the eggs. Photo taken by Tzu-Ruei Yang.

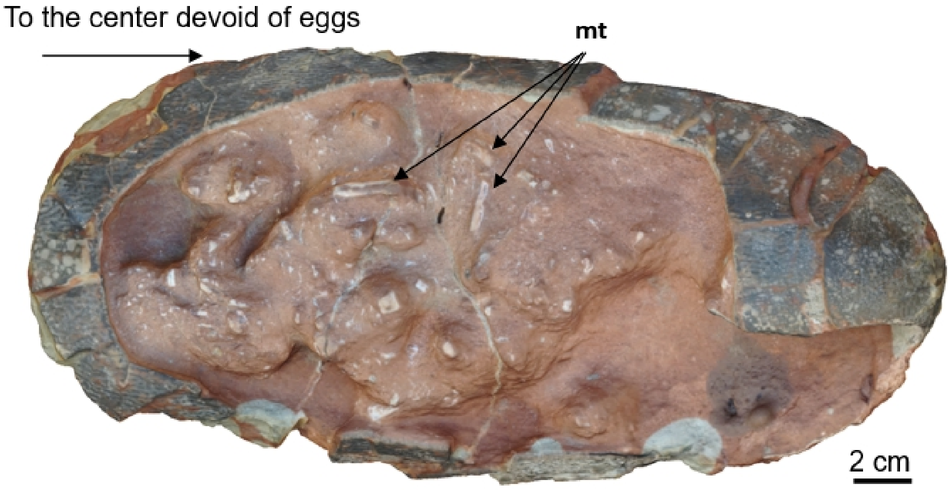


Figure 6-6 Oviraptorid egg containing scattered embryonic remains after preparation (egg I, SMNH-20140105-1) in a field-top view. The arrow points to the center of the original clutch, which can be identified by the blunt ends of the eggs. **Abbreviation**: **mt**, metatarsal. Scale equals 2 cm.

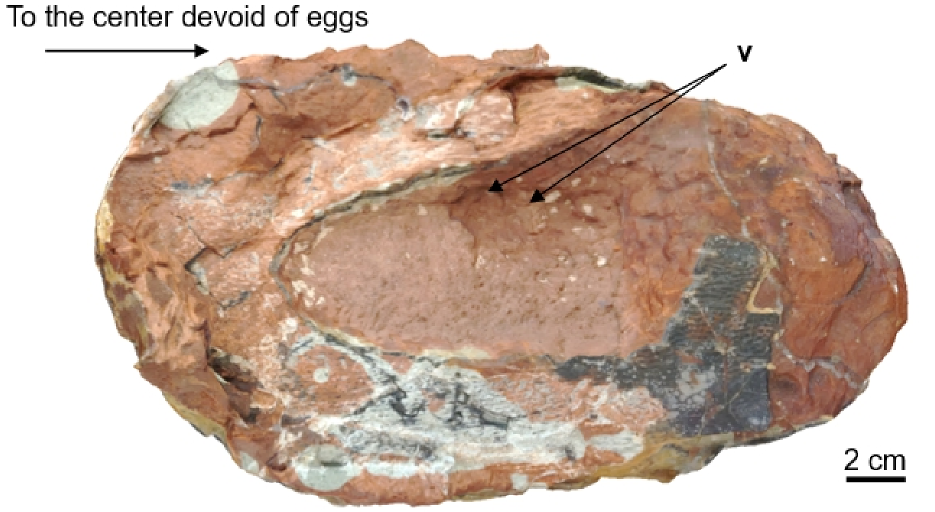


Figure 6-7 Oviraptorid eggs containing few embryonic remains (egg II, SMNH-20140105-2). This specimen is shown in a field-top view. The arrow points to the center of the original clutch, which can be identified by the blunt ends of the eggs. **Abbreviation**: **v**, vertebra. Scale equals 2 cm.

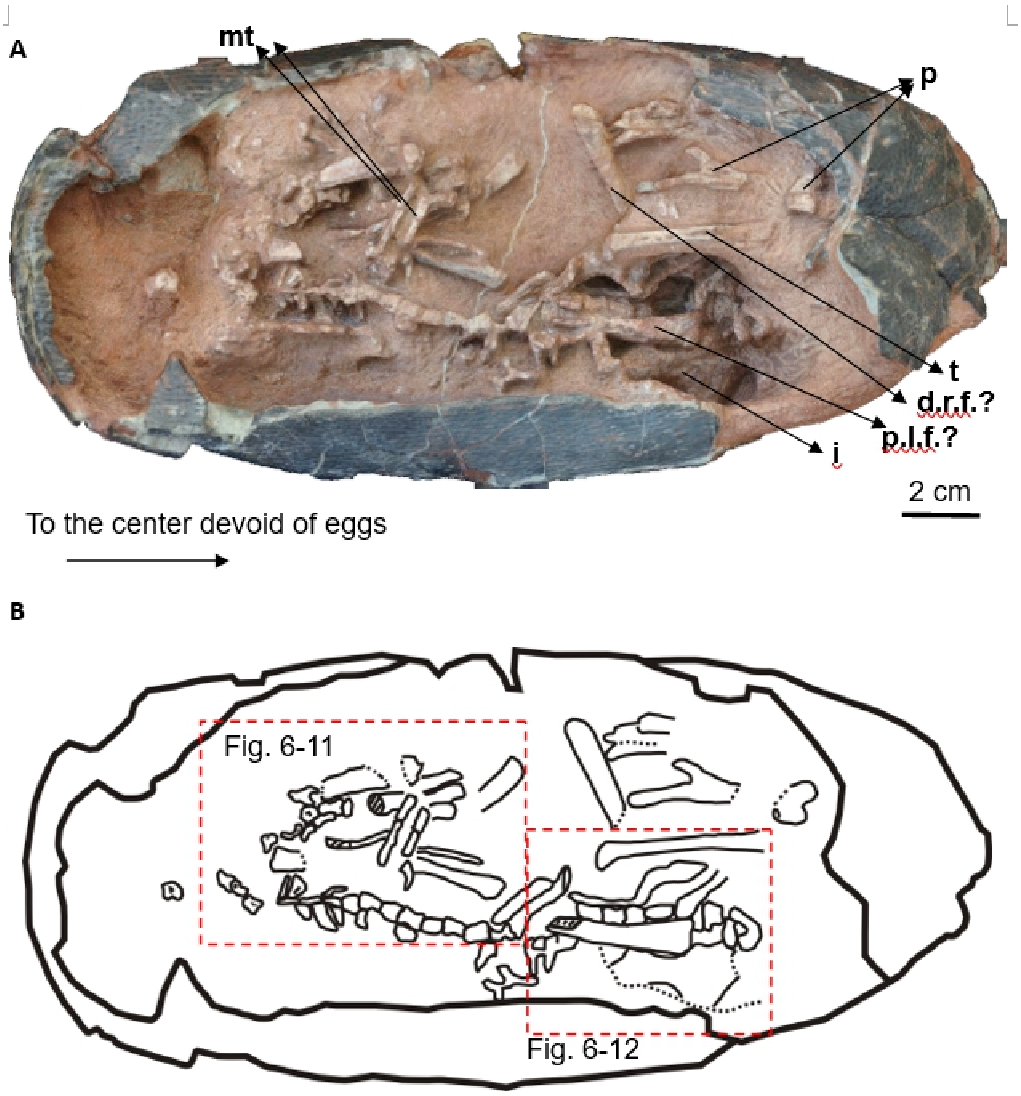


Figure 6-8 Oviraptorid egg containing a well-developed embryo after preparation (egg III, SMNH-20140105-3). The arrow points to the center of the original clutch, which is not observable now. (A) Photograph of the specimen SMNH-20140105-3 after the preparation. (B) **Abbreviation**: **d.r.f.**: distal part of right femur, **i**: ilium, **mt**: metatarsal, **p**: pubis, **p.l.f.**: proximal part of left femur, **t**: tibia. Scale equals 2 cm.

6-2-3 Taphonomic and Shell Histological Methods

Both taphonomic and shell histological features were employed in the identification of the developmental stage of each egg. Since all three eggs were preserved in the same block, the level of compaction should be similar. We estimate the level of compaction based on the same method illustrated in section 5-2-3 of this thesis. The shape of an egg viewed from the polar end is originally a circle but turned to an ellipse after compaction. We measured the long and short axes of each egg viewed from the acute end

(Appendices I-III). The factor of compaction was then calculated by dividing the difference between the length of the longer axis of the egg ellipse and the length of the shorter axis of the egg ellipse (as viewed from the polar end of the egg) by the restored egg diameter (the average of the length of the longer axis of the egg ellipse and the length of the shorter axis of the egg ellipse) (Table 6-1). We also compared the level of ossification of caudal vertebrae in each egg for further discussion.

In order to ootaxonomically assign the studied eggs and observe calcium removal from the innermost eggshell by the developing embryo (Chien, Hincke & McKee, 2009), eggshell samples were obtained from the midshaft zone of each egg. All eggshell samples were prepared as a petrographical thin section for histological observation under a polarized light microscope.

Table 6-1 Dimensions of each egg of the specimen SMNH-20140105.

Catalog number	Length (mm)	Width (mm)	Factor of compaction (%)
Egg I (SMNH-20140105-1)	184	82	30-32
Egg II (SMNH-20140105-2)	145	75	29-32
Egg III (SMNH-20140105-3)	165	74	30-33

6-2-4 CT Scanning

To obtain additional osteological information, egg III (SMNH-20140105-3) was scanned using X-ray micro-tomography at the Steinmann-Institute, Division of Paleontology, University of Bonn (Bonn, Germany). The scan was obtained with a Phoenix v|tome|x s (GE Phoenix X-ray; 240 kV) with a voltage of 170 kV and a current of 130 μA. The 800 images were obtained at a voxel size of 0.18528842, each with an exposure time of 400 ms. Three-dimensional reconstructions and measurements were generated using Avizo version 6.2.1.

6-3 Results

6-3-1 Taxonomic Assignment

The Nanxiong Group (treated as a formation in some of the references cited here), in which the specimen SMNH-20140105 was discovered, has yielded a great number of oviraptorid dinosaurs, including *Heyuannia huangi* (Lü, 2002), *Shixinggia oblita* (Lü & Zhang, 2005), *Banji long* (Xu & Han, 2010), *Ganzhousaurus nankangensis* (Wang et al., 2013b), *Nankangia jiangxiensis* (Lü et al., 2013a), *Jiangxisaurus ganzhouensis* (Wei et al., 2013), *Huanansaurus ganzhouensis* (Lü et al., 2015), *Tongtianlong limosus* (Lü et al., 2016), and *Corythoraptor jacobsi* (Lü et al., 2017). In addition, five embryo-containing eggs reported from the same group were assigned to *Macroolithus yaotunensis* and associated to *Heyuannia huangi* based on the geographical affinity to the fossil site of *Heyuannia huangi* (Cheng et al., 2008; Wang et al., 2016). Based on the shell microstructure, we assign all eggs in the specimen SMNH-20140105 to *Macroolithus yaotunensis*, which is produced by *Heyuannia huangi* according to (Cheng et al., 2008).

6-3-2 Shell Histology

All three eggs were so heavily compacted that the blunt end of each egg is not identifiable simply based on the geometrical shape; however, macroscopic features provide unequivocal evidence that allows for the identification. *Macroolithus* eggs have a blunt end that is covered by linearituberculate ornamentation, while the acute end lacks ornamentation (Zhao, 1975). The attitude of each egg is thus identified. Post-mortem manipulation or taphonomic disturbance is hence precluded since all blunt ends point in the same direction (Figure 6-5-Figure 6-8; Appendices I-III).

All radial sections of the eggshells from egg I, egg II, and egg III exhibit a distinct undulating boundary between the prismatic layer (PL) and mammillary layer (ML) (Figure 6-9). The thickness ratio of the PL to the ML ranges from 3.57 to 5.16. Based on the proportions of the remaining mammillary cone, we estimate that the ratio of prismatic layer to mammillary layer in egg III was 0.28-0.33 before resorption of the mammillary layer. The absence of all mammillary tips in egg II and egg III represents a significant calcium removal from the innermost shell, possibly by the developing embryos (Cheng et al., 2008). Thus, the comparison of mammillary intactness between egg I and eggs II/III suggests that eggs II/III are more developed than egg I (Figure 6-9).

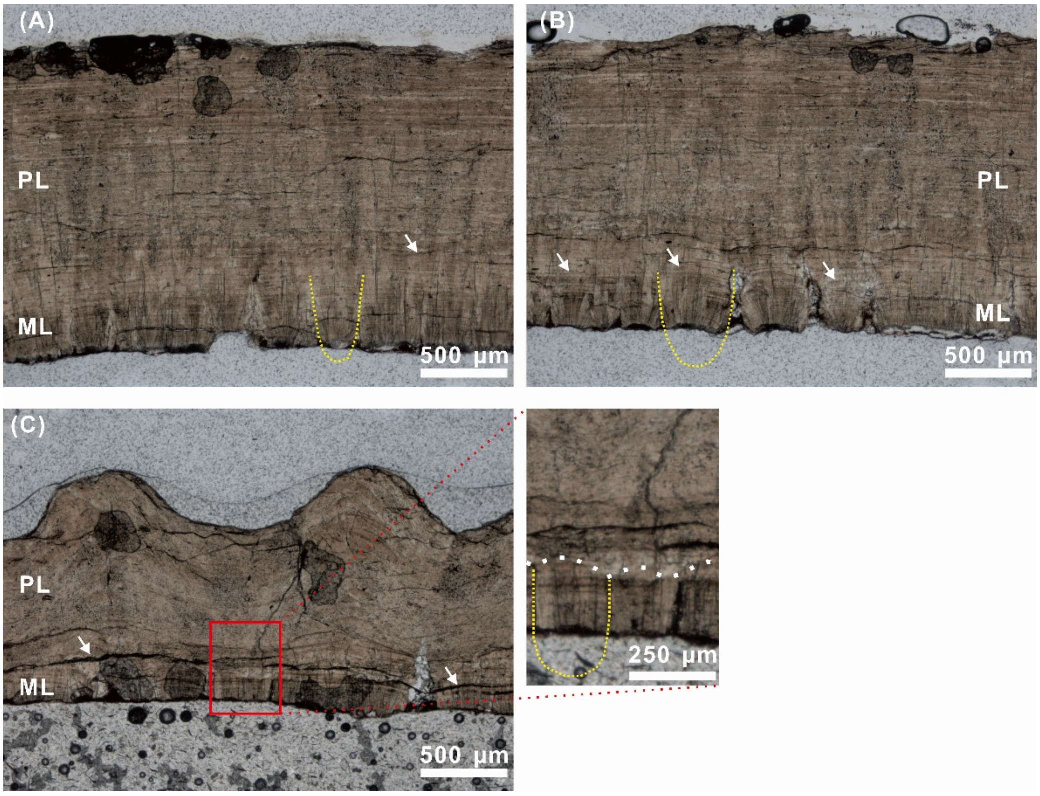


Figure 6-9 Photomicrograph of sectioned eggshells from (A) egg I, (B) egg II, (C) egg III, and (D) an enlarged section of the red column of (C). The undulating boundary between the PL and ML, as marked by arrows, is a distinct feature of *Macroolithus yaotunensis* (eggs of *Heyuannia huangi*). The mammillae were a cone-like structure as shown by yellow dash lines. The significant erosion of the mammillary layer shown by the absence of mammillary tip indicates calcium absorption of the developing embryo. Scale equals 500 μm.

6-3-3 Geopetal Features in SMNH-20140105 and Implications from Clutch Architecture

In comparison with well-preserved clutches (e.g., Figure 6-1), specimen SMNH-20140105 represents a partial clutch. The paired eggs (eggs II and III) represent a pair of siblings from the same oviposition that occurred before the individual egg (egg I). However, this temporal relationship can be only deduced by geopetal features together with the developmental stage of each egg. The specimen provides three geopetal features that allows for convincing identification of top and bottom. The first evidence is represented by the blunt end of an egg. In oviraptorid clutches, all eggs are arranged with their blunt ends pointing upwards and to the center devoid of eggs (Figure 6-1). The second geopetal feature is shown by the stacking pattern of the three eggs. In a well-preserved oviraptorid clutch that consists of several rings of eggs, the rings increase in size from lowest to highest. Based on the location of their blunt ends, eggs II and III are closer to the center of the clutch than egg I and thus are from a lower ring. The third feature is the location of the embryonic remains in each egg, which are expected to gravitationally accumulate at the bottom of the egg after death and disarticulation, coming to rest right atop the eggshell (Sander et al., 2008). The embryonic bones were not well visible in the specimen before preparation and separation into the individual eggs. The embryonic bone adjacent to the eggshell, which was revealed by preparing away the shell in all three eggs, thus must represent the lower side of the eggs (field-bottom). Based on these lines of evidence, we can reconstruct the stacking pattern and be assured that the paired eggs (egg II and egg III) were laid prior to the individual egg (egg I).

6-3-4 Egg I (SMNH-20140105-1)

Due to the incomplete preservation, the factor of compaction is estimated to be 30-35%. The embryo skeleton is disarticulated. Three metatarsal bones and scattered vertebra were recognizable but not osteologically assignable. Morphologically, egg I is larger than egg I and II, suggesting that egg I and the pair (egg II/egg III) were possibly laid by two different females in different body size because egg size is constrained by the size of female pelvis.

6-3-5 Egg II (SMNH-20140105-2)

Egg II and egg III are similar in size and factor of compaction. To keep egg II intact, mechanical preparation was only partially of the bottom side was only partially possibly and only scattered vertebrae were revealed in egg II. These vertebrae are recognizable as such but ill-defined (Figure 6-7).

6-3-6 Egg III (SMNH-20140105-3)

Egg III preserves numerous recognizable postcranial remains. The CT scan revealed a bone aggregation near the blunt end, possibly representing the cranial part of the embryo (Figure 6-10). However, cranial parts were not exposed by preparation. Neutron imaging or synchrotron tomography might be able to resolve the possible preservation of the cranial parts in the matrix. The sacral region is possibly represented by four vertebrae (v1-v4) exposed in lateral view close to the possible ilium (Figure 6-8 & Figure

6-12). However, sacral ribs are not recognizable. A total of 15 caudal vertebrae (Ca1-Ca15) are preserved in lateral view in a continuous series, extending to the acute end of the egg in egg III (Ca1 to Ca15 in Figure 6-11). The size of the caudal vertebrae decreases from Ca1 to Ca15, indicating that the Ca15 is reasonably the posteriormost vertebra among them. The neural arch is absent in all caudal vertebrae except for Ca9, possibly due to poor preservation or incomplete ossification. Right next to the series of caudal vertebrae is there an aggregation of right ulna, two radii, and scattered metatarsals. The right ulna is possibly identified based on it unmatured distal styloid process and its relative position to other skeletal remains. Both radii were recognizable since they present distinct styloid process of the distal end. The left radius possibly broke during fossilization. The distal part of the right femur is recognizable on the basis of its shape in the lateral view; however, the head of the proximal embryonic femur is not well formed. The proximal part of left femur is also visible, an interpretation based on the proximity of the bone to the ilium and more pronounced shape of the head. However, the length of both femora cannot be measured. The distal part of a tibia in the posterior view can be identified as well, based on the medial malleolus. Only the proximal halves of the left metatarsals are preserved in the egg III.

While the cranial parts of the embryo in egg III are not visible, the pose of the embryo inside the egg is indicated by the orientation of the caudal vertebrae (Figure 6-8) which indicates that the cranial parts of the embryo were near the blunt end of the egg, i.e., in the direction of the center of the clutch.

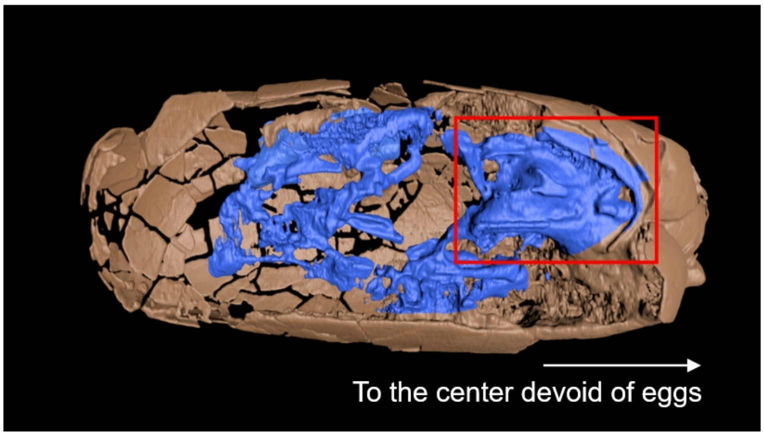


Figure 6-10 Micro-tomographical image of egg III (SMNH-20140105-3). The aggregation pointed to by the red arrow probably represents the cranial parts of the embryo, indicating the pose of the embryo inside the egg. The white arrow points to the center of the original clutch, which is not observable now.

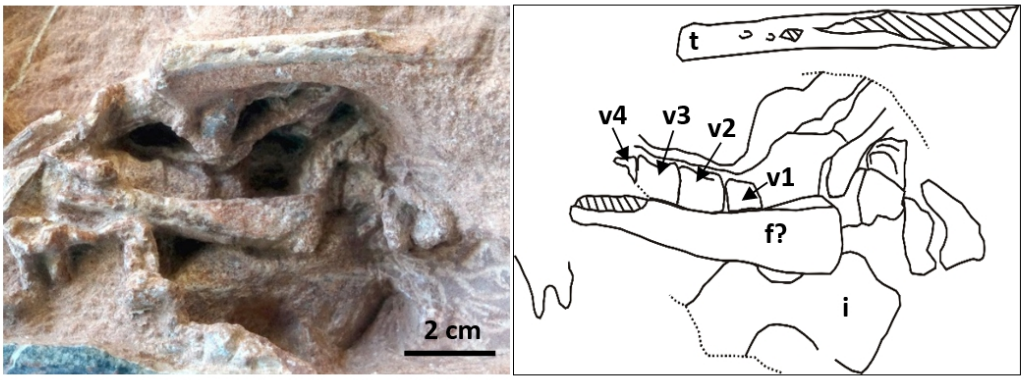


Figure 6-11 Pelvic region of the oviraptorid embryo in the egg III. **Abbreviation**: **f**: femur, **i**: ilium, **v**: vertebra, **t**: tibia. Scale equals 2 cm.

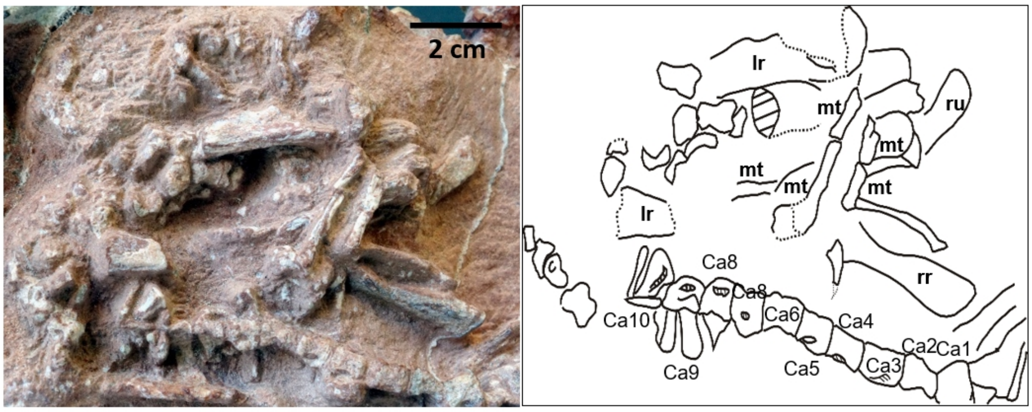


Figure 6-12 Caudal region of the oviraptorid embryo in the egg III. **Abbreviation**: **Ca**: caudal centrum; **mt**, metatarsal; **lr**, left radius; **rr**, right radius; r**u**, right, ulna. Scale equals 2 cm.

6-4 Discussion

6-4-1 Taxonomy of Embryos and Ootaxonomy of Eggshells

Since the skull in all eggs of the studied clutch SMNH-20140105 is absent or unexposed, these specimens would have been considered as Oviraptoridae *incertae sedis*, pending new information. Despite numerous contemporaneous oviraptorid dinosaurs unearthed from the same formation, none of them was associated to an ootaxon in the absence of embryo-containing eggs except for *Heyuannia huangi* NMNS-0015276-F02-embryo-01 of Cheng et al. (2008) Thus, based on the egg shape (Table 6-1 & Table 6-2), histological and surficial features of eggshell (Figure 6-9 and Table 6-2), and the geographical affinity, we prefer to assign these oviraptorid embryos to *Macroolithus yaotunensis*, which is laid by *Heyuannia huangi* (Cheng et al., 2008).

In comparison with other previously described embryo-containing eggs, the shell of egg III shows similar ratios of PL to ML and microstructural features to the specimen NMNS-0015276-F02-embryo-01 of Cheng et al. (2008). In addition, the specimen NMNS-0015276-F02-embryo-01 of Cheng et al. (2008) and the three embryos of Wang et al. (2016) were discovered in adjacent localities. Although Wang et al. (2016) did not assign the specimens IVPP V20182, IVPP V20183, and IVPP V20184 to any ootaxon, these embryo-containing eggs are assignable to *Macroolithus yaotunensis* based on their microstructural features and geographical affinity (personal communication with S. Zhang).

6-4-2 Embryo Position *In Ovo*

The *Beibeilong* embryo reported by Pu et al. (2017) provided a superb analog to interpret the position of oviraptorid embryo *in ovo*. Oviraptorosaurian embryos exhibit a similar position *in ovo* to modern chickens—cranial parts toward the blunt end of the egg and caudal end near the acute end. Although the cranial part of the embryo is not exposed by mechanical preparation, we are able to identify the *in ovo* position of the embryo based on the direction where the caudal vertebrae extend (Figure 6-8 & Figure **6-12**). Furthermore, the CT image of egg III reveal an aggregate of skeletal remains near the blunt end, possibly representing the cranial part of the embryo. The embryonic skull located near the blunt end indicates that the perinate would have to hatch from the blunt end. This observation concurs with the hypothesis that oviraptor clutch were partially exposed to the air, but with the acute ends buried in substrate (Chapter 5; Wiemann et al., 2017).

Table 6-2 Parameters of eggshell microstructures in comparison with previously reported specimens.

Catalog number	*Egg length (mm)*	*Egg width (mm)*	*Thickness of prismatic layer (mm)*	*Thickness of mammillary layer (mm)*	*Ratio of PL to ML*	*Ootaxonomic assignment*	*Reference(s)*
SMNH-20140105-3	165	74	1.25-1.45	0.3-0.4	3.6-4.1	*Macroolithus yaotunensis*	This study
IGM 100/979	180	65					Norell et al. (1995)
IVPP V9608	150	55	0.55	0.2	3.7		Dong & Currie (1996)
IGM 100/971	120	60*			3.7	Elongatoolithidae indet. or *Elongatoolithus elongatus*	Norell, Clark & Chiappe (2001)
MPC-D100/1017			0.48	0.19-0.33	1.5-2.5	Elongatoolithidae indet.	Weishampel et al. (2008)
NMNS-0015276-F02-embryo-01	175.3	92.1	0.96-1.35	0.24-0.44	3.1-4	*Macroolithus yaotunensis*	Cheng et al. (2008)
MPC-D100/1017			0.48	0.19-0.33	1.5-2.5	Elongatoolithidae indet.	Weishampel et al. (2008)
IVPP V20182	198.3	88.0				Elongatoolithidae indet., but very possibly *Macroolithus yaotunensis***	Wang et al. (2016)
IVPP V20183	179.5	92.1	0.96-1.32	0.24-0.44	3.3-4	Elongatoolithidae indet., but very possibly *Macroolithus yaotunensis***	Wang et al. (2016)
IVPP V20184	163.5	74.8				Elongatoolithidae indet., but very possibly *Macroolithus yaotunensis***	Wang et al. (2016)

*Estimated value **Based on personal communication with S. Zhang.

6-4-3 Hatching Asynchrony Inferred from SMNH-20140105

Hatching asynchrony can be inferred if embryos of different developmental stages are present in a single clutch, provided that the embryos developed continuously and at the same rate and that there was no developmental arrest. The lack of developmental arrest is inferred from phylogeny (Williamson et al., 2017). The presence of different developmental stages can be determined based on the size of skeletal elements and histological examinations (Weishampel et al., 2008). However, these methods are not possible in the present specimens since they do not preserve the same skeletal parts. Instead, our inference of hatching asynchrony is mostly based on the level of articulation. The taphonomic influence on the level of articulation is here precluded since all eggs have similar factors of compaction and were preserved in the same block, which represent the same taphonomic history and deformation. Kundrát et al. (2008) categorized therizinosauroid embryos into four stages based on the level of ossification and the degree of aggregation of skeletal remains. The first stage consists of poorly articulated skeletal remains that are clustered in an aggregation on the corner of the egg. Kundrát et al. (2008) interpreted the aggregation as a result of the confinement by the yolk. However, the aggregation could be also a result of gravitational accumulation after death and disarticulation, which was not considered by Kundrát et al. (2008). Whereas the aggregation was not observed in our studied specimen, we observed that all embryonic remains sit near the bottom of the eggs in this study, indicating a gravitational accumulation instead of a confinement by the yolk.

Hamburger & Hamilton (1951) divided the developmental history of a chicken embryo into 46 stages over 20-21 days. Embryological studies have revealed that the anterior vertebral column develops earlier than the posterior part (Diwan & Dhakad, 1995). Somite formations reaches the tip of pygostyle at stage 22 (3.5 days). In egg III, the caudal vertebrae are articulated and well developed, indicating that the embryo was near the hatching stage. Egg I only preserved scattered vertebrae that are ill-defined, presumably because of poor ossification or preservation. The latter factor is here precluded because all eggs have similar factors of compaction and were preserved in the same block, which represent the same taphonomic history and deformation. Egg III was prepared from both sides, ensuring the best exposure of all embryonic remains. The one preserved metatarsal in egg I is slimmer than all of the metatarsal bones in egg III, supporting our interpretation that egg III is more developed than egg I. Besides, the observation of different developmental stages in the three eggs demonstrates a temporal gap between the two eggs in the inner (lower) ring and the one in the outer (upper) ring. Our study thus provides supportive evidence to Yang et al. (2018b)'s observation that oviraptorid dinosaurs laid the innermost, lower ring of eggs first, covered this ring with substrate, and then laid the second ring, or even third ring, of eggs. However, due to the lack of matching skeletal parts, an estimation of the length of the gap between the two laying events in our specimen (egg I vs. eggs II and III) is not possible.

6-4-4 Hatching Asynchrony as a Synapomorphy in Oviraptorids

Weishampel et al. (2008) described four oviraptorid embryo-containing eggs, possibly from the same clutch, but refrained from assigning them to a particular species due to the immaturity of the bones and poor preservation. Based on the assumption that the four embryo-containing eggs were from the same clutch, they hypothesized hatching asynchrony in oviraptorids. The four embryo-containing eggs were discovered in the Nemegt Formation of Bugin-Tsav, Mongolia, which was tentatively dated to a 72.0-70.8 Ma interval (late Campanian; Ogg, Agterberg & Gradstein, 2004). Oviraptorids from Mongolia include *Ingenia* sp., *Rinchenia mongoliensis*, *Avimimus nemegtensis*, *Nomingia gobiensis*, and cf. *Elmisaurus* (and possibly other unknown species), all of which have been described from the Nemegt Formation in Bugin-Tsav, Mongolia (reviewed in Funston et al., 2017), indicating a large number of sympatric species. Our specimen, likewise, could potent pertain to any of a number of species reported from Nanxiong Group (Campanian—Maastrichtian) of Jiangxi and Guangdong Provinces, China. However, the comparison of egg shape and eggshell microstructure strongly supports the assignment of SMNH-20140105 to *Heyuannia huangi*. If the hatching asynchrony reported by Weishampel et al. (2008) is true, hatching synchrony may well be a shared character among Oviraptoridae.

The latest phylogeny of modern birds on the basis of genomic analyses shows that hatching asynchrony is only observed in Neornithes (Stoleson & Beissinger, 2010; Prum et al., 2015). All sauropods are considered to lay a whole clutch *en masse* (Reisz et al., 2012), and the eggs from the same clutch hatched synchronously as modern reptiles in the absence of incubation behaviors. Among theropods, so far, only *Troodon* eggs have been suggested to hatch synchronously (Varricchio & Jackson, 2003). The evidence from our study demonstrates the earliest hatching asynchrony in the dinosaurian lineage.

6-4-5 Insights into the Existing Ecological Hypotheses

Ecologists formulate hypotheses and then test these hypotheses by ecological experiment or observations in the field. However, due to the limitations of the fossil record, these reproductive ecological hypotheses are rarely testable when dealing with extinct animals. Adult-associated oviraptorid clutches discovered in China and Mongolia have been suggested to represent evidence for an avian mode of incubation (Norell et al., 1995; Dong & Currie, 1996; Fanti, Currie & Badamgarav, 2012). However, this hypothesis has been challenged by several subsequent studies (Martin & Simmons, 1995; Deeming, 2002a). Yang et al. (2018b) suggested an alternative hypothesis that the clutch-associated adults were actually females in the process of laying eggs.

However, it is obvious that oviraptorid dinosaurs exhibited a more refined nesting strategy compared to ground-nesting reptiles. Wiemann et al. (2017) detected two pigments in *Heyuannia huangi* eggshells from Henan, Jiangxi, and Guangdong Provinces of China, indicating that these oviraptorid dinosaurs had evolved colored eggs to enhance their reproductive success. Besides, the reevaluation of shell porosity in Wiemann et al. (2017) suggested an open nesting mode. Egg coloration is considered as an adaption for preventing embryos in a vulnerable open nest from predators (Kilner, 2006). The colored oviraptorid eggs in an open nest thus hint at relatively higher risks during embryo development. To conclude, insights arising from this study, adult-associated clutches, and pigmented eggshells support the “nest failure hypothesis.” for explaining hatching asynchrony in oviraptors. Ill supported statement.

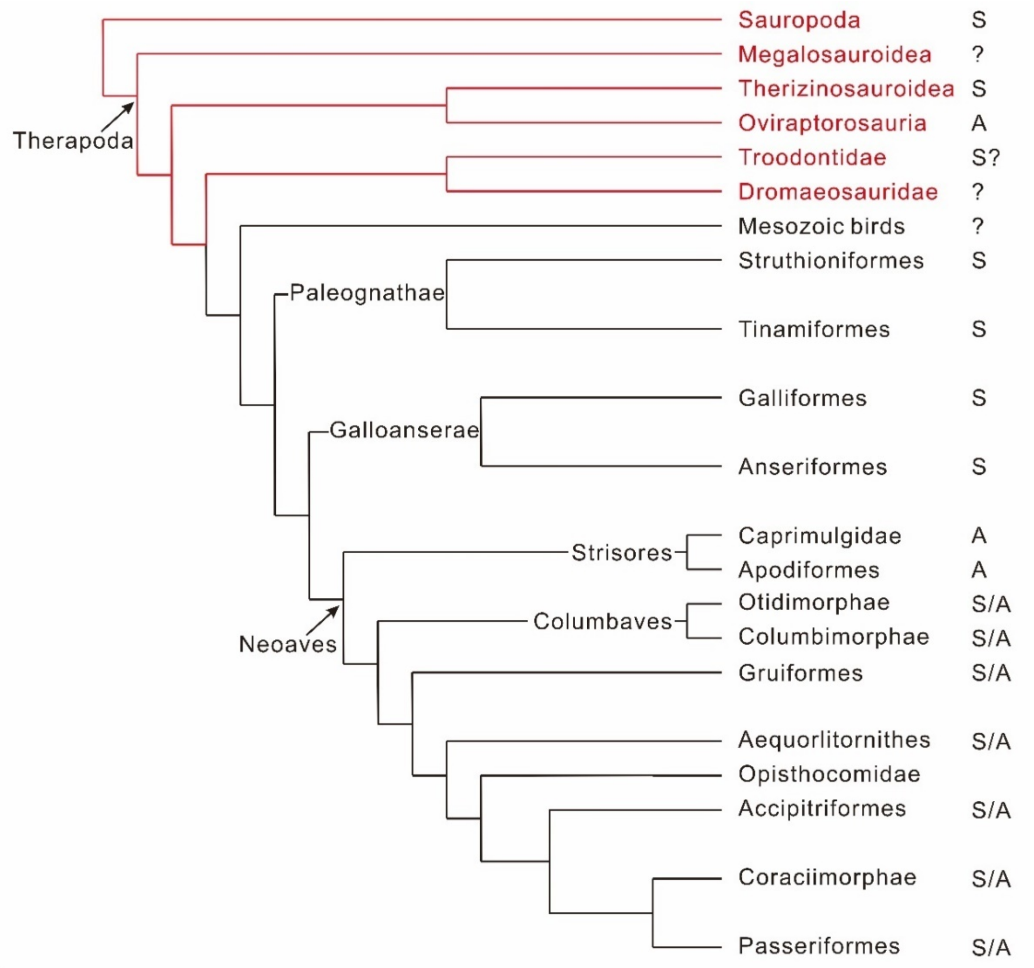


Figure 6-13 Distribution of hatching modes (S, synchronous hatching; A, asynchronous) among saurischian dinosaurs based on the fossil record for non-avian dinosaurs and on Stoleson & Beissinger (2010) for birds. The phylogeny was compiled by integrating the latest avian phylogeny (black, Prum et al., 2015) and a general dinosaur phylogeny (in red).

6-4-6 Brooding and Polygamy Behaviors

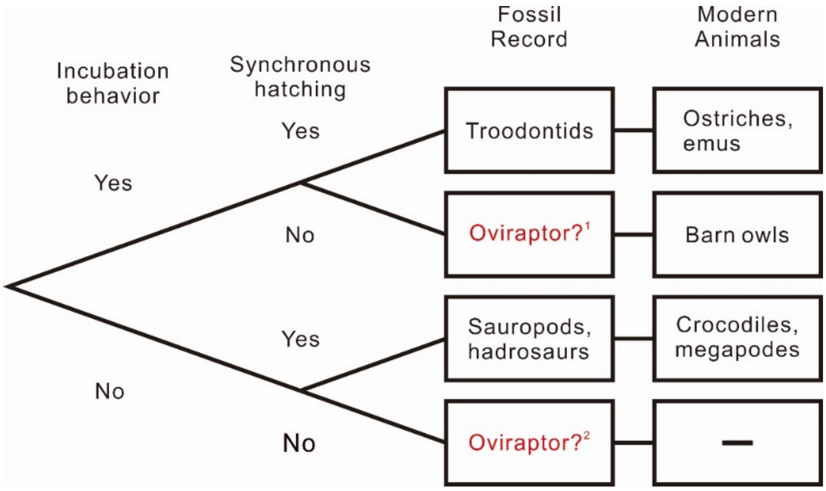
The hatching asynchrony in oviraptorids inferred from our study represents new evidence to the interpretation of the adult-associated clutches and can be explained by two inferences. First, if oviraptorids did utilize contact incubation, then oviraptorids were analogous to some modern birds such as barn owls that exhibit extreme hatching asynchrony (Wilson, Wilson & Durkin, 1986). In combination with the hypothesis that oviraptorids were polygamous and the male was in charge of incubating the whole clutch (Varricchio et al., 2008; Moore & Varricchio, 2016), the male may have started incubation before several females completed the clutch. Furthermore, the hatching asynchrony in oviraptorids can be explained by invoking above hypotheses (section 6-1-4).

Chapter 6: Hatching Asynchrony

Prior to the discussion of second inference, how a clutch was finished should be discussed. If a three-ring clutch were contributed by three females, each of which contributes a ring of eggs from inner to outer sequentially, the hatching asynchrony would have been simply caused by the time interval between two contributions from two females. Nevertheless, an elemental study by Yang et al. (2016) demonstrates that multiple females contributed to eggs in the same ring, thus precluding the assumption that a female contributes a ring of eggs.

Second, as discussed previously in Chapter 5, if there was no contact incubation for oviraptorids, the hatching asynchrony may be a result of the time interval between different ovipositions or egg rings. However, the multiple-ring arrangement in oviraptorid clutches could evolve because of selective advantages of hatching asynchrony. This peculiar strategy is not observed in any modern animals (Fig. 6-14), which would suggest that the nesting behaviors of oviraptorids is not analogous to that of any modern animals and that it may be difficult to use it to test any hypotheses for modern birds (section 6-1-4).

Following the conclusion arising from our previous study (Chapter 5), the second inference is preferred in the absence of contact incubation. Amiot et al. (2006) and Eagle et al. (2015) also partly supported the second inference by indicating a lower incubation temperature than modern birds. Although we precluded the first inference, the second inference is still pending validation, possibly based on further future studies. Since shell microstructure is a reliable indicator the embryo developmental stage, the level of resorption shown by the shell of every egg from a clutch would potentially test the possibility. More practically, a more complete clutch with embryos is the best material to validate our hypothesis.



[1] If oviraptorids did contact incubate their eggs, the hatching asynchrony likely resulted from the incubating adult starting incubation before the clutch was completed.

[2] If oviraptorids did not contact incubate their eggs, the hatching asynchrony was simply a result of the time interval between different ovipositions.

Figure 6-14 The four possible combinations of incubation mode and hatching mode in oviraptors, *Troodon*, and modern reptiles and birds.

6-5 Conclusion

Oviraptorids are a bizarre group of dinosaurs, whose nesting behaviors remains challenging to understand despite many well-preserved specimens. The partial clutch containing embryonic remains, reported in this study, provides further support to the hypothesis of hatching asynchrony in oviraptorid dinosaurs. Despite the uncertainty about the precise taxonomic assignment within Oviraptoridae, this specimen from southern China demonstrates that the hatching asynchrony can be traced far back in time to oviraptorid dinosaurs and may be a shared derived character of oviraptorid dinosaurs. The pose of the embryo in our study indicates that the perinate hatched from the exposed blunt end where the center of clutch would have been. This observation concurs with the reconstruction of a partially open oviraptorid clutch based on egg coloration, eggshell porosity analysis, and clutch architecture.

Oviraptorid dinosaurs exhibited peculiar and unique nesting strategies that is not analogous to any modern animals. Oviraptorid reproductive biology serves as a warning that simply using a “bird model” vs. a “crocodile model” to infer behaviors of extinct animals is problematic. However, oviraptorid dinosaurs may have been able to diversify due to their unique nesting biology, including some key adaptations such as colored eggs, hatching asynchrony, communal nesting behavior, polygamous behavior, and so on.

Chapter 7 Synthesis: the reproductive biology of oviraptorid dinosaurs

PUBLICATION

Yang T-R and Sander PM. A review of the reproductive biology of oviraptorid dinosaurs. (to be submitted)

ABSTRACT

Among all dinosaurs, the Late Cretaceous oviraptorid dinosaurs, in addition to troodontid dinosaurs, boast the best fossil records ranging from numerous eggs to abundant embryos, seven clutch-adult associations, highly organized egg clutches, two gravid adults, possible colonial nesting grounds, and plenty of species described from skeletons from China and Mongolia. In combination with cutting-edge chemical analytical techniques and new perspectives, these well-preserved fossils provide insights into reproductive biology, ecology, behavior, and developmental biology of oviraptorid dinosaurs, contributing to several groundbreaking paleontological discoveries in the last decade. Some of the discoveries received further supports, while others remain controversial, indicating that a comprehensive, rigorous reexamination using all available evidence is required. In a recent review, oviraptorid dinosaurs were considered as an intermediate stage in moving toward the modern avian reproduction mode and it was assumed that their reproductive biology can be inferred based on the avian model.

This chapter will review evidence generated by previous studies on oviraptorid dinosaurs, in combination with new research in this dissertation. In addition, with respect to reproductive biology, we also briefly compare oviraptorid dinosaurs with another well-studied dinosaur group — troodontid dinosaurs. This new evidence and comparisons illuminate the peculiar reproductive biology of oviraptorid dinosaurs, and hence open up a new avenue for understanding the behavior and ecology of

this unusual dinosaur group. Based on all these lines of evidence, oviraptorids had an essentially unique reproductive biology lacking modern analogous. Simply applying either avian or reptilian models to infer the biology of extinct animals thus appears inappropriate in the case of oviraptorids.

Chapter 7: Synthesis

7-1 Introduction

Oviraptorosauria, a group of feathered maniraptoran dinosaurs from the Cretaceous period, consists of several subgroups such as Oviraptoridae and Caenagnathidae. With several crucial fossil discoveries in the past, oviraptorids yield the best fossil record for elucidating the reproductive biology of any dinosaur group. Previous studies of these discoveries hypothesized that some distinct avian traits such as a toothless beak (Wang et al., 2017b; Wang, Zhang & Yang, 2018), monoautochronic ovulation, brooding, and polygamous behavior had appeared in the Cretaceous oviraptorids. Hence, more and more studies imposed avian models on the Cretaceous oviraptorids and inferred their biology based on the modern bird analog. Regarding reproductive biology, a recent review by Varricchio & Jackson (2016) suggested that the Cretaceous oviraptorids were intermediate in their reproductive biology between primitive reptilians and derived Neornithes. Some hypotheses that oviraptorids exhibited avian traits were supported by our new evidence, while some were challenged. Thus, a comprehensive, rigorous reexamination using all available evidence is required. In this chapter, we will re-examine and review previous studies regarding the reproductive biology of oviraptorid dinosaurs and compile the new evidence that has emerged from previous chapters (Chapters 2-6). Our synthesis broadens Varricchio and Jackson's (2016) review and demonstrates that oviraptorid dinosaurs exhibit a peculiar reproductive biology that is not analogous to that of any modern animals.

7-2 Distribution and Diversity of Oviraptorid Dinosaurs

Oviraptorid dinosaurs were exclusively reported from Cretaceous formations of Asia, especially China and Mongolia. So far, there are 18 genera described, forming a spatially constrained monophyletic group (Figure 7-1). Although there were three oviraptorosaurs reported from Argentina (Frankfurt & Chiappe, 1999), Australia (Currie, Vickers-Rich & Rich, 1996), Brazil (Frey & Martill, 1995), all of them were reexamined and reinterpreted as pertaining to other theropod dinosaur taxa. Thus, Oviraptoridae is still a distinct group only from East Asia. A recent study by Funston et al. (2017) reviewed the discoveries of oviraptorid dinosaurs from the Nemegt Basin. Their study posited a high diversity of oviraptorid dinosaur in the Nemegt Basin during the Late Cretaceous.

Although no studies have investigated the Nanxiong Formation in southeastern China with similar methods used in Funston et al. (2017), it is obvious that southeastern China was also a prosperous habitat that harbored many oviraptorid dinosaurs (Figure 7-1). Such a prosperous habitat is also present in modern birds. In the Himalayas, more than 460 different songbird species live in a narrow band stretching from eastern Nepal through China, India, and Myanmar (Price et al., 2014). Price et al. (2014) found the evidence for the niche-filling hypothesis based on data from Himalayan songbirds. The ecological competition for resources ultimately drove the speciation of songbirds in Himalayas. The high diversity of songbirds in a narrow region is like the one of oviraptorid dinosaurs in Nemegt Basin and southeastern China during the Late Cretaceous. The coexistence of these different species can be explained through dietary niche partitioning (Funston et al., 2017).

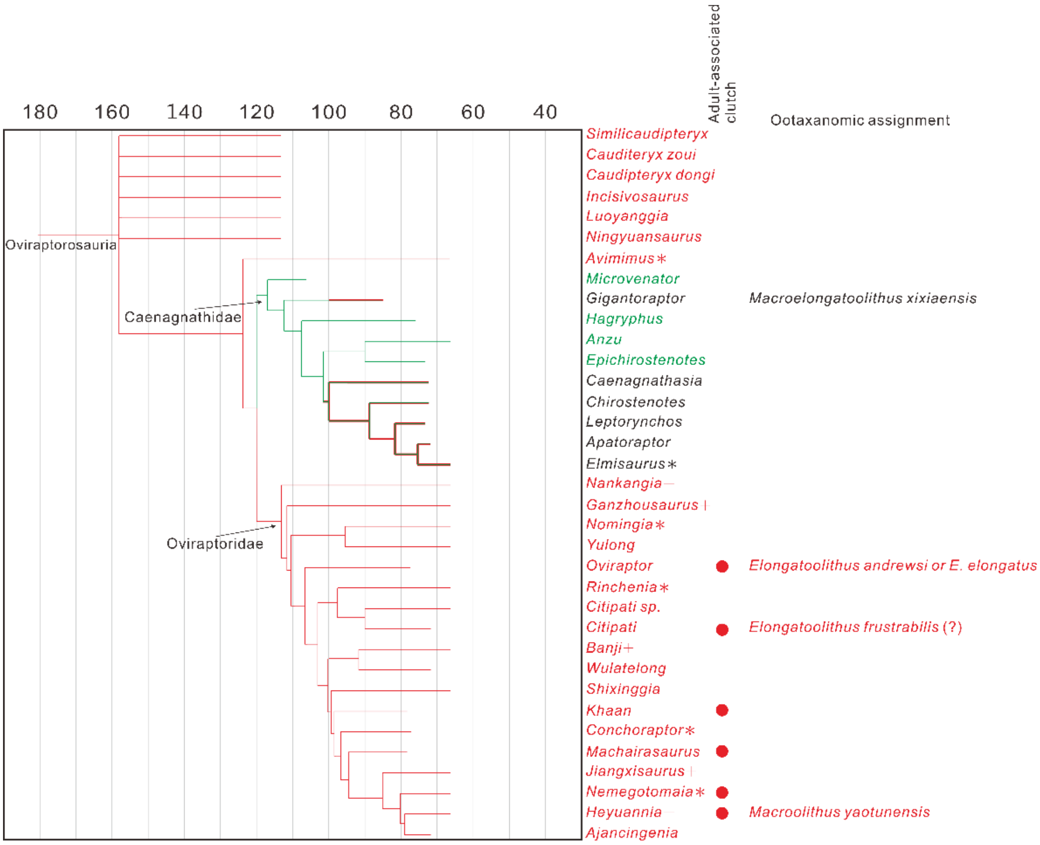


Figure 7-1 Time-calibrated phylogeny of oviraptorosaurs. The Asian taxa are marked in red, and the North American ones are marked in green. Taxa marked in black have been discovered in both Asia and North America. All clutch-adult associations were discovered in China or Mongolia and assigned to Oviraptoridae as indicated by red circles. Annotations: *, Nemegt Basin, southern Mongolia; +, Nanxiong Formation in southern China. Modified from Funston et al. (2017).

7-3 Review of Evidence on Oviraptorid Clutch Parameters

7-3-1 The Architecture of an Oviraptorid Clutch

The first oviraptor clutch was described along with the report of the holotype of *Oviraptor philoceratops* (Osborn, 1924); however, clutch architecture was not investigated at that time, nor until the early 1990s. Thus, Sabath (1991) was the first scientific report that attempted to depict the clutch architecture and taphonomy of an oviraptorid clutch based on the clutch specimens ZPAL MgOv-II/23 (for collections acronyms, see section 1-5) from the Gobi Desert, Mongolia. His reconstruction suggested that an oviraptorid clutch was completely buried in decaying vegetation matter and sediment (Figure 7-2; Table 7-1). The eggs in the oviraptorid clutch were depicted as arranged in pairs, organized in a ring, and oriented nearly vertical with tilting outward at a small angle with their acute ends pointing downwards and to the center devoid of eggs (Figure 7-2; Table 7-1; Sabath, 1991). The paired arrangement was echoed by the discovery of an oviraptorosaurian pelvis with a pair of eggs inside from the Nanxiong Group of Jiangxi Province, China (NMNS-VPDINO-2002-0901; Sato et al., 2005).

Later, based on a well-preserved clutch-adult association specimen ("Big Mamma", IGM 100/979; Figure 7-3), Norell et al. (1995) presented an illustration of a "brooding" oviraptor atop a sediment-free, randomly arranged clutch, which is similar to the egg arrangement of modern ground-nesting birds such as ostriches. Notably, the significant paired arrangement of eggs and center devoid of eggs, as numerous oviraptorid clutches and Sabath (1991) previously had documented, were absent in Norell et al. (1995)'s illustration.

Based on another clutch-adult association specimen (IVPP V9608; Figure 7-4; Table 7-1), Dong & Currie (1996) slightly amended Norell et al. (1995)'s illustration by emphasizing the paired arrangement; however, some characters were still missing in Dong & Currie (1996)'s reconstruction. For instance, the multiple-egg-ring arrangement was missing, possibly because the specimen preserves only six eggs.

In 2002, Deeming (2002a) suggested a new reconstruction from an ornithological perspective (Figure 7-5; Table 7-1). Deeming (2002a)'s reconstruction was solely rooted in Sabath (1991). Although the reconstruction was still incorrect since the blunt end of the eggs point outward and the eggs are buried, Deeming (2002a)'s reconstruction revived the egg-free center that was absent in Norell et al. (1995) and thus argued against the incubation behavior hypothesized by Norell et al. (1995) (see the detailed discussion about brooding and incubation behavior in sections 5-1-1 and 7-5-2). The egg-free center suggests that an effective heat transfer from the brooding adult to the clutch was implausible (Deeming, 2002a). Moreover, the idea that the eggs in an oviraptorid clutch were buried was introduced based on the assumption of a buried nesting mode of Sabath (1991) and porosity data from Mou (1992). However, Mou (1992)'s porosity data, that was based on a single piece of eggshell, probably was subject to a sampling bias because Varricchio et al. (2013) revealed the heterogeneous distribution of porosity by sampling the eggshell all over a single *Troodon* egg. Thus, Yang et al. (2015) analyzed the porosity pattern of an oviraptorid egg and suggested a semi-open nesting mode. Based on another clutch-adult association, Fanti, Currie & Badamgarav (2012) proposed a new reconstruction of the oviraptorid clutch from the sedimentological aspect. Their reconstruction presented a partially-open nesting mode in oviraptorid dinosaurs (Figure 7-6). This hypothesis was echoed by two recent studies based on the discovery of tetrapyrrolic pigments preserved in eggshells (Wiemann et al., 2017) and updated porosity data (Yang et al., 2015). Based on this, Wiemann et al. (2017) and Tanaka et al. (2018) provided an almost accurate reconstruction (Figure 7-7; Table 7-1). Both reconstructions (Wiemann et al., 2017; Tanaka et al., 2018) illustrated the appearance of an oviraptorid egg well; however, the clutch architecture still requires improvement since the semi-open nesting mode was not well presented in both reconstructions (Wiemann et al., 2017; Tanaka et al., 2018). Therefore, Tanaka et al. (2018) applied a completely open nesting mode in their reconstruction and considered that eggs were brooded by the oviraptorosaur adult as indicated by several oviraptorid clutch-adult associations. Tanaka et al. (2018) further suggested that the enlargement of the central opening in clutches of larger eggs, which were laid by larger oviraptorosaurs, represents an adaption that allows brooding behavior and reduce the load on the eggs.

Finally, a detailed investigation of complete clutches by Yang et al. (2018b) revealed several general features of the oviraptorid clutch. To summarize, a complete oviraptorid clutch contains >30 eggs (>15 pairs) on a mound. The paired eggs are arranged in three to four superimposed rings with their blunt ends leaning at an angle of >40 degrees to the ground towards the clutch center devoid of eggs (Figure 7-8). The blunt ends were exposed to the air and the acute ends of all eggs were buried in sediment (Yang et al., 2018b). The authors also observed sediment interbedded between the different layers of eggs, which should be part of the original clutch architecture and not added by sedimentary processes after abandonment of the clutch.

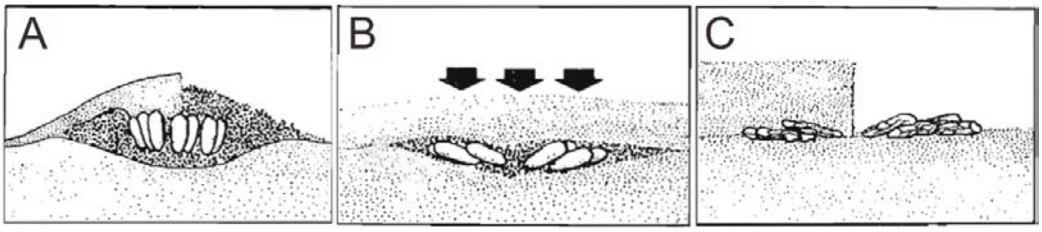


Figure 7-2 The first reconstruction of an oviraptorid clutch by Sabath (1991). (a) In the beginning of fossilization, the oviraptorid clutch was buried in soil and sediment. Note that the eggs were nearly vertically oriented with a slight outward inclination, the acute ends point to the center, and that there are two pairs of eggs. (b) The compaction compresses the egg clutch and make the eggs nearly horizontally inclined. (c) The final appearance of an oviraptorid clutch as it is excavated. Modified from Sabath (1991).

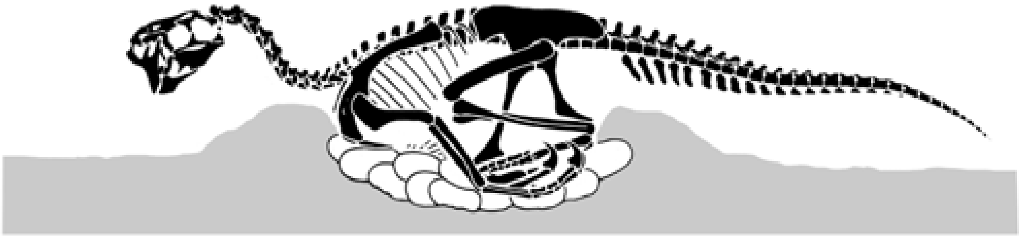


Figure 7-3 The depiction of an oviraptorid clutch as part of the reconstruction of a brooding oviraptor by Norell et al. (1995). The IGM 100/979 specimen, on which the reconstruction is based, consists of a partial adult oviraptorid and an incomplete clutch. Note that the eggs are not covered and randomly arranged. Reproduced from Norell et al. (1995).

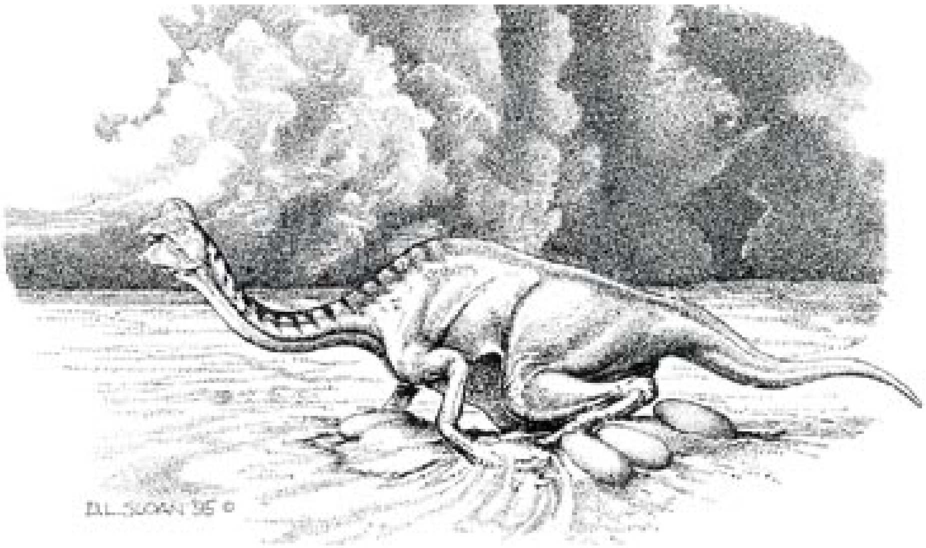


Figure 7-4 The depiction of a brooding oviraptor by Dong & Currie (1996). In this reconstruction, the eggs are arranged at least partially in pairs in a nearly horizontal position in a partially open nest, yet it is unclear if the blunt end or the acute end of the eggs points to the clutch center. Reproduced from Dong & Currie (1996).

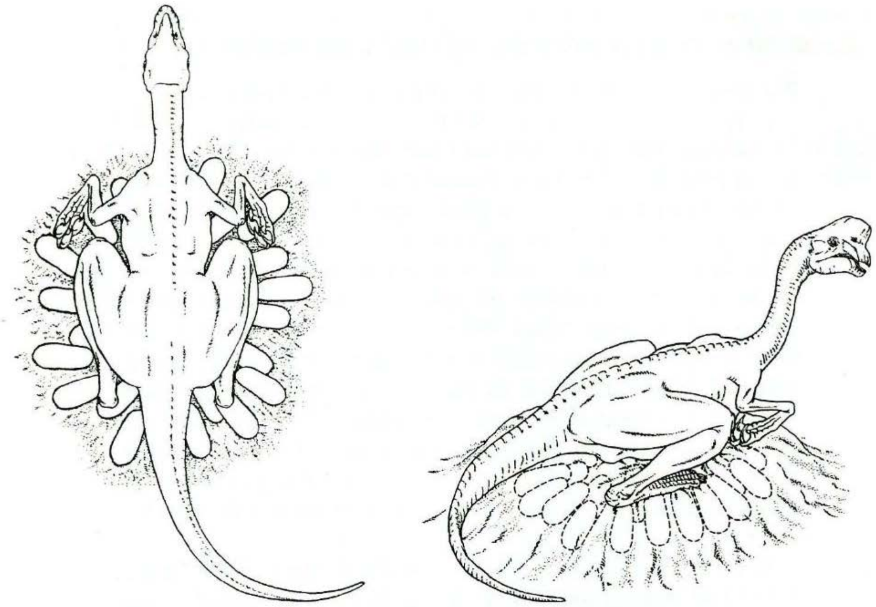


Figure 7-5 A reconstruction of brooding oviraptor atop a clutch by Deeming (2002a). Note that the blunt end of the eggs point outward as like the reconstruction by Sabath (1991). However, the inclination of the eggs is higher than the ones in (Figure 7-2; Sabath, 1991).

Figure 7-6 Recent artist's reconstruction of *Nemegtomaia*, courtesy of Michael B. H. (https://commons.wikimedia.org/wiki/File:Nesting_Nemegtomaia.jpg) based on Fanti, Currie & Badamgarav (2012) and Wiemann et al. (2017). Note that the arrangement of clutch is upside down, with the eggs inclined outwards and the pointed end directed upward. This is also the first reconstruction that shows integumentary appendages (filamentous feathers and planar feathers) in the adult. Note that the eggs are pigmented based on the evidence for biliverdin preservation in the *Macroolithus yaotunensis* eggs (Wiemann et al., 2017) (see discussion below).

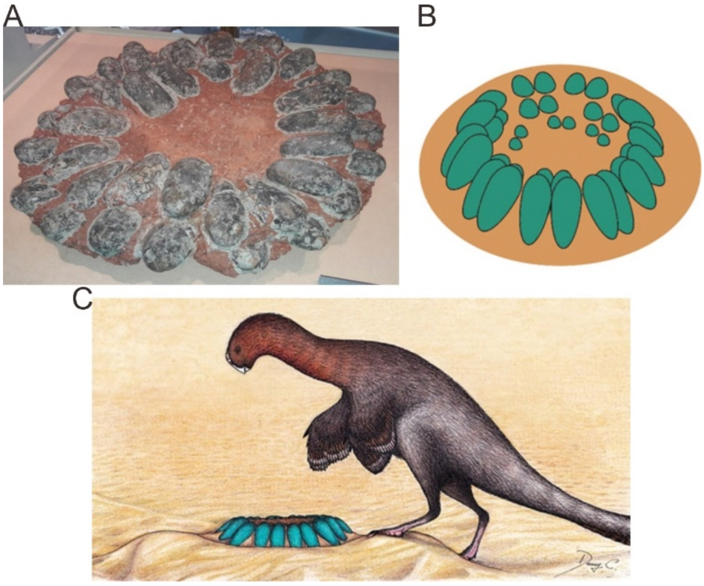


Figure 7-7 (a) A complete oviraptorid clutch (AGM 4990). The clutch was discovered in the Late Cretaceous Gaogou Formation in Henan Province, China, and was prepared from the field bottom. This clutch represents a standard example that includes all necessary characters. It consists of >40 eggs (>20 pairs) with their blunt ends pointing toward to the center devoid of eggs. (b) The clutch is inferred to haven been partially exposed to the air based on the discovery of pigments preserved in eggshells and investigation of complete oviraptorid clutches (Wiemann et al., 2017). (c) The most correct artist's reconstruction of an oviraptorid clutch and adult to date, that of *Heyuannia huangi* and its egg clutch by Danny Cicchetti (https://commons.wikimedia.org/wiki/File:Heyuannia_and_eggs_nest.jpg) based on Wiemann et al. (2017). However, this reconstruction still lacks some distinctive features of oviraptorid clutches such as multiple rings of eggs, which are present in (b).

Table 7-1 Previous reconstructions of oviraptorid dinosaur clutch architecture.

	Orientation of eggs	Paired arrangement	Blunt ends point inward and acute ends outward	Multiple egg rings	Completely buried, partially buried, or completely open	Mound or pit	Egg color
Sabath (1991)	Vertical	Yes	No	No	Completely buried	Mound	No
Norell et al. (1995)	Horizontal	No	No	No	Partially buried	Pit	No
Dong & Currie (1996)	Nearly horizontal	Yes	No	No	Partially buried	Mound	No
Deeming (2002a)	Oblique	Yes	No	Yes	Completely buried	Mound	No
Fanti, Currie & Badamgarav (2012)	Nearly horizontal	Yes	Yes	No	Partially buried	Mound	No
Wiemann et al. (2017)	Oblique	Yes	Yes	Yes	Partially buried	Mound	Yes
Tanaka et al. (2018)	Oblique	Yes	Yes	No	Partially buried	Mound	Yes

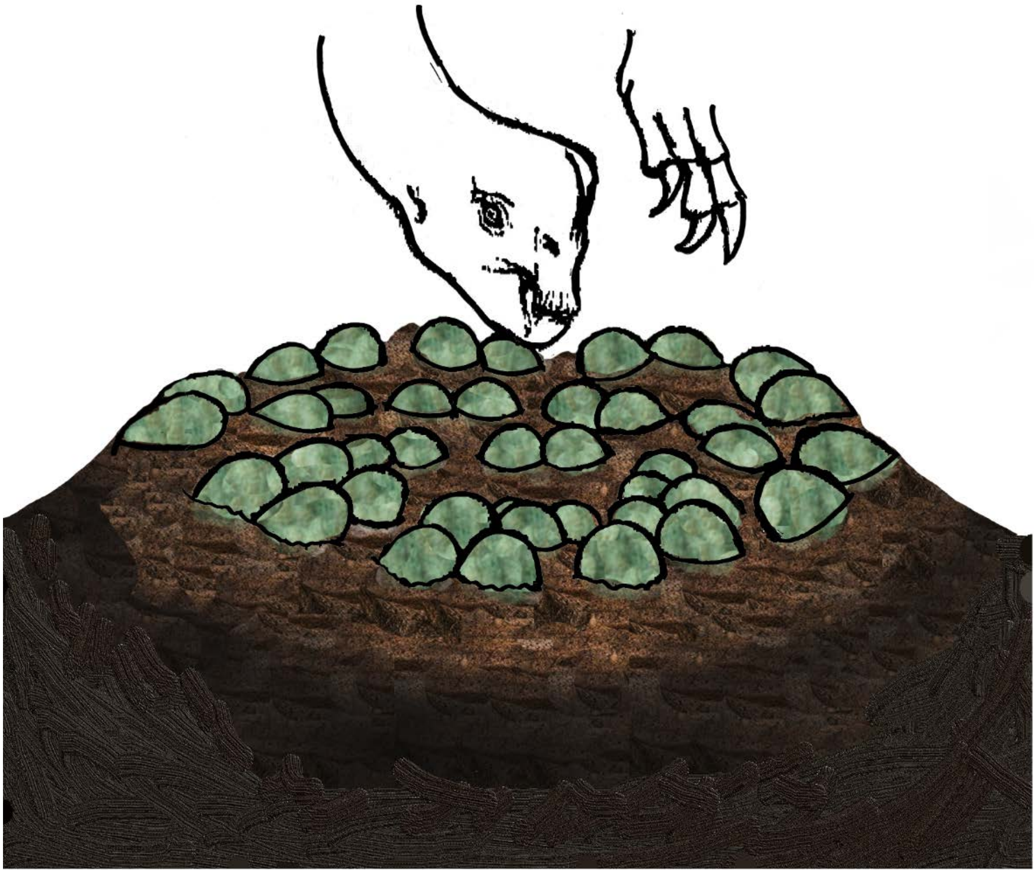


Figure 7-8 Final reconstruction in Yang et al. (2018b). Note that the eggs are partially buried.

7-3-2 Relative Clutch Size and Ovulation Mode in Oviraptorids

In the literature on reproductive biology, clutch size refers to the number of eggs and the total mass of eggs laid in a single brood by a nesting bird or reptile. It is well known that clutch size increases with body size in modern amniotes (Blueweiss et al., 1978), like other life history variables. The allometry of body size and clutch size in modern organisms was frequently studied (Blueweiss et al., 1978; Ford & Seigel, 1989; Kulesza, 1990; King, 2000), yet rarely in dinosaurs. A limited amount of studies attempted to interpret dinosaur reproductive biology based on allometric studies or in situ observation of dinosaur clutches. These allometric studies suggested that the ratio of adult size to clutch size of sauropods is significantly smaller than in all other archosaurs (Seymour, 1979; Sander et al., 2008; Werner & Griebeler, 2011). Sander et al., (2008, p. 99 – 102) and Ruxton, Birchard & Deeming (2014) further suggested that the relatively smaller clutch size of sauropods is a result of their splitting of a clutch among several nests or several oviposition events per year, also resulting in several nests per year. Their hypothesis also implied that a sauropod clutch was completely laid by a single female, as suggested by Varricchio & Jackson (2003). Conversely, the relative and absolute size of an oviraptorid clutch was rarely discussed in the literature despite the abundant fossil record. Varricchio et al. (2008) compared clutch volume–adult body mass ratios of birds, dinosaurs, and crocodiles and observed a relatively high ratio in oviraptorid and troodontid dinosaurs, close to that seen in modern birds exhibiting paternal care and communal nesting behavior. Thus, they suggested that oviraptorid and troodontid dinosaurs displayed communal nesting behavior and paternal care. Their hypothesis of communal nesting behavior was later supported by element analyses of eggshells from the same clutch in eggs of the same pair and of different pairs. Specifically, phosphorus distribution across the eggshell thickness, which is an indicator of female age, is the same within pairs but differs between pairs (Yang et al., 2016). Since eggs of the same pair were certainly laid by the same female, this suggests that different pairs were laid by different females. Thus, the several complete oviraptorid clutches from China described in Yang et al. (2018b) were possibly laid by several females communally.

Modern crocodiles have two functional oviducts, each laying multiple eggs per oviposition, whereas birds lost one oviduct and lay only one egg per oviposition. This suggests that the evolution of ovulation mode from crocodiles to modern birds is a result of oviduct regression and egg number decrease. An oviraptorosaurian pelvis with a pair of eggs inside confirms egg number decrease (Figure 7-9; Sato et al., 2005); however, conclusive evidence for oviduct regression is still lacking. A specimen of the long bony-tailed *Jeholornis* and two enantiornithine birds from the Early Cretaceous in northeastern China showed preservation of ovarian follicles on the left side of their bodies (Zheng et al., 2013). Being within the phylogenetic bracket of oviraptorid dinosaurs and Mesozoic birds, troodontid dinosaurs thus probably play an important role in oviduct regression (Figure 7-10). A recent review paper concluded that *Troodon* clutches from North America display a similar paired arrangement of eggs, multiple egg rings, and inward-pointing blunt ends of eggs (Varricchio & Jackson, 2016), indicating a similar nesting mode to that of oviraptorid dinosaurs. However, troodontid clutches from China and Mongolia lack paired arrangement, possibly supporting our previous speculation that one of the two reproductive tracts in Asian troodontid dinosaurs had already regressed and reached the avian mode (Zheng et al., 2013). The fossil record is consistent with what we observe in modern birds. The kiwi (*Apteryx*) is the only modern birds that retains two functional ovaries, yet only one of them is functional during the reproduction season (Kinsky, 1971). This observation in kiwi birds suggests that the reduction of the right oviduct might well have preceded the reduction of the right ovary (Kinsky, 1971).

The most popular hypothesis suggested that oviduct regression in modern birds evolved for weight reduction for active flight (Zheng et al., 2013; Johnson, 2014). A different hypothesis proposed that the presence of a single oviduct constrains calcification to a single egg at a time and therefore minimizes physical contact between eggs that could lead to malformations (Guioli et al., 2014). Both hypotheses require testing by more evidence from various perspectives, and thus the selective advantage for oviduct reduction remains unclear.

Figure 7-9 An oviraptorosaurian pelvis with a pair of shelled eggs inside (NMNS-VPDINO-2002-0901, Sato et al., 2005). Scale bar, 10 cm.

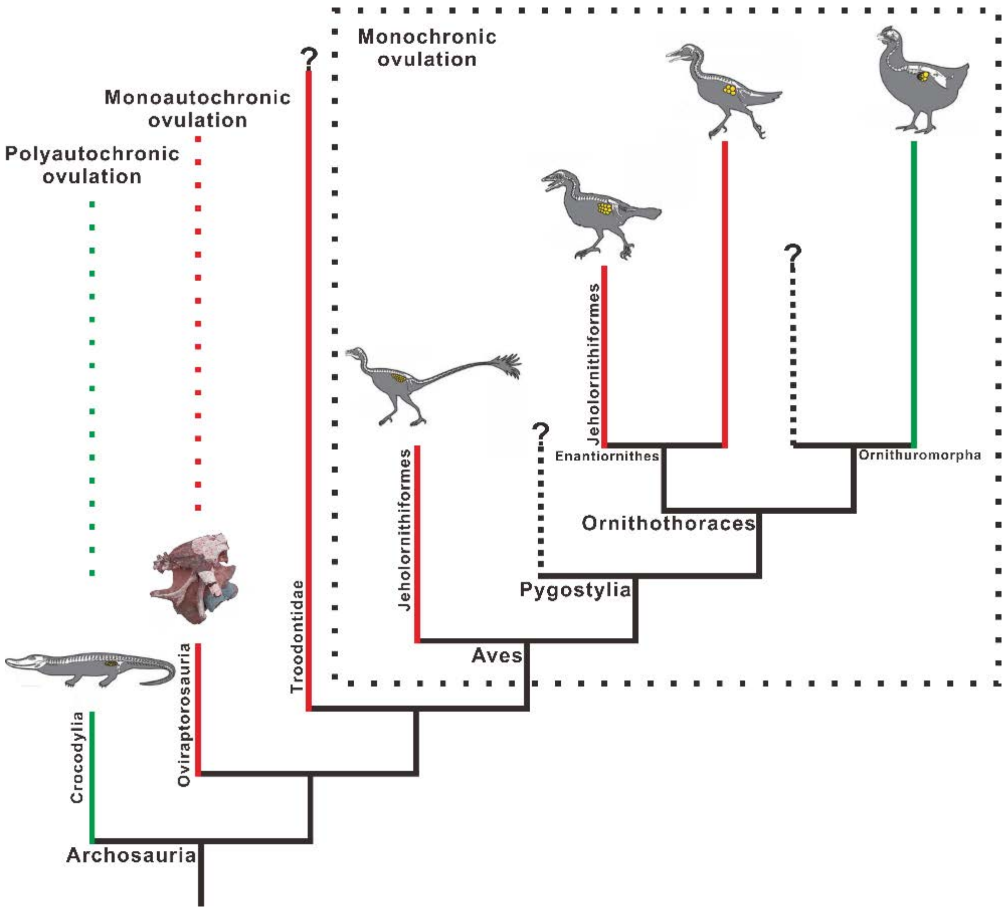


Figure 7-10 A simplified cladogram of archosaur relationships on the line to modern birds and different ovulation modes. Green lines indicate living lineages and red lines refer to extinct taxa. Modified from Zheng et al. (2013). Polyautochronic ovulation is defined as having two functional oviducts producing multiple eggs in an *en masse* oviposition. Monoautochronic ovulation is defined as having two functional oviducts, each producing one egg per oviposition; and monochronic ovulation is defined as having one functional oviduct that produces one egg per oviposition.

7-4 Understanding the Oviraptorid Dinosaur Egg

7-4-1 Ootaxonomy of Oviraptorid Eggs

All Mesozoic dinosaurs were oviparous, the same as their closest living relatives, crocodiles, and modern birds. Dinosaur eggs vary greatly in appearance, shape, and size. Unlike modern amniotic eggs, fossil eggs were taxonomically ill-defined and rarely explicitly assigned to a biological species. In the early 1970s, Heinrich Karl Erben attempted to establish a classification system. Based on eggshell microstructure, Erben & Münzenburg (1970) assigned testudoid eggs from France/Spain to type A and C and the ornithoid eggs from Mongolia to type B. However, Erben, Hoefs & Wedepohl (1979) discarded types A and C and reassigned the testudoid eggs from France/Spain to a single type, which demonstrates the confusion arising from such a simplistic classification system.

In the same period, Zikui Zhao from the IVPP of Beijing, China, developed a modern parataxonomic system in the 1970s. Zhao (1975) described egg features, such as egg size, ornamentation of the eggshell, and microstructure of eggshell units, and used these in parataxonomic diagnoses, facilitating the communication between paleontologists in discussion of fossil eggs. However, most of his research was published in Chinese, hindering the spreading of his parataxonomic system. Based on these egg features, Zhao (1975) assigned the elongate eggs from southern China to the first official ootaxanomic family—Elongatoolithidae. This ootaxanomic family was linked to Oviraptorosauria based on a oviraptorid embryo-containing egg discovered in the Gobi Desert (Norell et al., 1994).

Later, the Russian paleontologist Konstantin Mikhailov followed Zhao's work and published a review paper entitled "Fossil and recent eggshell in amniotic vertebrates: fine structure, comparative morphology and classification" in 1997 (Mikhailov, 1997). His work formalized egg parataxonomy, erecting different oofamilies in addition to egg species, enabling scientists to study fossil eggs according to the International Code of Zoological Nomenclature. Mikhailov (1997) recognized six basic structural morphotypes among amniote eggs, including geckonoid, testudoid, crocodiloid, dinosauroid-spherulithic, dinosauroid-prismatic, and ornithoid, the last four of which pertain to archosaurs. Carpenter (1999a) reviewed this egg parataxonomy system and attempted to link ootaxanomic families to taxonomic groups based on the basic structural morphotypes. The elongatoolithid eggs were assigned to the ornithoid egg type, implying a phylogenetic affinity between theropods and modern birds (Carpenter, 1999a).

The egg parataxonomy also contributed to the correction of the hypothesis that an *Oviraptor* was stealing a clutch of *Protoceratops* eggs. Oviraptor, means "egg thief" in the *derivatio nominis* of Osborn (1924) due to his mistaken assignment of oviraptor eggs to *Protoceratops*. The discovery of an oviraptorid embryo-containing egg (Norell et al., 1994) and an oviraptor adult sitting atop a clutch Norell et al. (1995), in combination with the ootaxonomic assignment, suggested that *Oviraptor* may have been a loving mother instead of an egg thief.

Among all oofamilies, the Elongatoolithidae was most frequently reported from China and Mongolia. Currently, the Elongatoolithidae contains the oogenera *Nanhsiungoolithus* (Zhao, 1975), *Elongatoolithus* (Zhao, 1975), *Macroolithus* (Zhao, 1975), *Macroelongatoolithus* (Li, Yin & Liu, 1995), *Ellipsoolithus* (Mohabey, 1998), *Trachoolithus* (Carpenter, Hirsch & Horner, 1994), *Heishanoolithus* (Zhao & Zhao, 1999), *Ornitholithus* (Dughi & Sirugue, 1962), *Paraelongatoolithus* (Wang et al., 2012), *Undulatoolithus* (Wang et al., 2013a), *Rodolphoolithus* (Vianey-Liaud & Garcia, 2003), *Spongioolithus* (Bray, 1999), *Porituberoolithus* (Zelenitsky, Hills & Currie, 1996), and *Continuoolithus* (Zelenitsky, Hills & Currie, 1996). Some of these such as *Elongatoolithus*, *Macroolithus*, *Macroelongatoolithus*, are thought to have been laid by oviraptorids based on clutch-adult associations or embryo-containing eggs (Figure 7-1; Osborn, 1924; Norell et al., 1995; Dong & Currie, 1996; Clark et al., 1999; Cheng et al., 2008; Weishampel et al., 2008; Fanti, Currie & Badamgarav, 2012; Wang et al., 2016; Pu et al., 2017; Norell et al., 2018). Although other elongatoolithid ootaxa are valid genera, they have not been assigned to specific dinosaur species. It is therefore hard to exclude the possibility that they were all produced by oviraptorid dinosaurs as well since they exhibit similar ornamentation of surface and egg shape to those of known oviraptorid eggs. More studies are needed for assigning an egg (ootaxon) to a specific oviraptorid dinosaur.

7-4-2 The Structure of the Archosaur Egg

All archosaur eggs have a biomineralized, layered eggshell that is composed of calcium carbonate (calcite) crystals embedded in an organic matrix. The hard-shelled egg with several membranes and complicated internal structure is an adaption for terrestrial animals to protect their embryo from predation and dehydration, and enhance the reproductive success (Geist & Ruben, 2004). The biomineralized eggshell displays various structural morphotypes and different numbers of crystallized layers, which are used for ootaxonomic assignment (Mikhailov 1997). Despite various egg types, all archosaur eggs possess a mammillary layer as the base for eggshell growth and pores for gas exchange across the eggshell. Compared with geckonoid, testudoid, and crocodiloid eggs, dinosaur eggs (dinosauroid-spherulithic, dinosauroid-prismatic, and ornithoid), for instance, oviraptorid eggs, show a prismatic layer underlying the mammillary layer. Ornithoid eggs have an external layer in addition to the mammillary and prismatic layers, which is a distinctive feature restricted to avian eggshells. However, a study by Varricchio, Horner & Jackson (2002) described a putative external layer in *Troodon* eggshells, currently the only non-avian dinosaur egg displaying the external layer. Eggshell microstructure thus corroborates that oviraptorid dinosaurs lie within the phylogenetic bracket of birds and crocodiles. It is very likely that the features shared by the eggs of birds and crocodiles, such as *membrana testacea* and cuticle, were present in dinosaurs as well.

The single-layered shell membrane (or two-layered shell membrane in birds), also called as *membrana testacea*, underlying the biomineralized eggshell, is a structure for protecting the embryo from bacterial or fungal invasion (Palmer & Guillette, 1991). Packard & DeMarco (1991) investigated the fine structure of *membrana testacea* in extant eggs. The *membrana testacea* is composed of fibrous proteins such as collagen type I and thus shows a fibrous pattern (Wong et al., 1984).

Another organic layer, the cuticle layer, present in some birds, overlies the calcitic eggshell. The cuticle layer is often described as "waxy" due to its high amount of lipids, which keep the internal fluids from evaporating and therefore protect the encased embryo from desiccation. In addition to lipids, the avian cuticle contains proteins, polysaccharides, calcium carbonate (vaterite), calcium phosphates (hydroxyapatite, HAp), and pigments (Wedral, Vadehra & Baker, 1974; Nys et al., 1991; Packard & DeMarco, 1991; Dennis et al., 1996; Mikhailov & Ornithologists' Club, 1997; Fraser, Bain & Solomon, 1999; Cusack, Fraser & Stachel, 2003; Igic et al., 2015). Basically, the cuticle is divided into two distinct layers, including an amorphous HAp/vaterite inner layer and a proteinaceous outer layer (Simons, 1971; Dennis et al., 1996; Fraser, Bain & Solomon, 1999). The inner cuticle layer is composed of needle-like HAp/vaterite crystals in some avian eggs but present in the form of nanospherical HAp/vaterite in other avian eggs (Dennis et al., 1996; D'Alba et al., 2014).

In extant bird eggs, an air space forms in the egg when the contents of the egg cool and contract after laying. The air cell lies between the outer and inner *membrana testacea* layers at the egg's blunt end. This structure provides the embryo with oxygen when it is ready to start breathing on its own and hatch from the egg (Vleck & Hoyt, 1991). The air cell thus plays an important role in the transition from chorioallantoic to pulmonary respiration (Seymour, 1984). Most reptilian eggs do not form air cells, possibly because they only have a single shell membrane (outer and inner membranes fuse together) (Packard & DeMarco, 1991). The existence of an air cell might depend on eggshell porosity and developmental mode of the embryo. Rokitka & Rahn (1987) found that in bird eggs, the shell overlying the air cell has a greater pore density than the remainder of the shell. Moreover, the air cell also prevents the inside of the eggshell overlying the air cell (blunt end) from being eroded by the developing embryo (Booth, 1989), thus providing an empirical method to test the existence of an air cell in fossil eggs (see below).

The chalaza is a structure only present in avian eggs, which has not been reported in extant reptilian eggs (Ferguson, 1982). In the eggs of most birds, chalazae are two spiral proteinaceous bands of tissue that anchor the yolk in a fixed place in the albumen. Almost all avian eggs must be turned during incubation (Poulsen, 1953), and the chalazae play a crucial role for protecting the embryo from deleterious adhesion to the shell membranes during turning (New, 1957). By contrast, turning during incubation is fatal to reptilian embryos, and the adhesion of the embryo to the shell membrane is common as well. The possible presence of chalazae in non-avian dinosaur eggs is discussed below.

The color of all reptile eggs is the white of the calcium carbonate of the shell or apatite of the cuticle. However, virtually all birds, especially passerines, produce colored eggs employing two specific pigments—biliverdin and protoporphyrin (Kennedy & Vevers, 1976). Protoporphyrin is a reddish-brown heme precursor, while biliverdin is a blue–greenish heme catabolite (Ryter & Tyrrell, 2000). Even nearly white bird eggs contain these pigments in low concentrations. The function of the color is visual signaling and camouflage of an egg clutch. In addition to signaling and camouflage, numerous other functions of egg color pigments have been proposed, such as antimicrobial effects (Ishikawa et al., 2010), protection from solar radiation (Lahti, 2008), and eggshell mechanical reinforcement (Gosler, Higham & Reynolds, 2005). These functions may explain why even white-colored bird eggs contain biliverdin and protoporphyrin.

7-4-3 Egg Shape, Albumen, and Yolk in Oviraptorid Eggs

All oviraptorid eggs are extremely elongate, presenting a smooth acute and an ornamented blunt end. Previous studies suggested that the elongate egg shape was an adaptation for maximizing egg size relative to pelvic canal size and thus body size.

Elongate eggs thus would have accommodated more resources for the developing embryo (Grellet-Tinner et al., 2006; Dyke & Kaiser, 2010). Osteological and histological studies of oviraptorid embryonic remains revealed a precocial developmental pattern, implying the necessity of containing a large amount of albumen or yolk *in ovo* in support of the developing embryo (Cheng et al., 2008; Weishampel et al., 2008; Wang et al., 2016). However, Deeming & Ruta (2014) proposed that, in contrast to modern birds, albumen was absent in elongate eggs (i.e., oviraptorid eggs), which would have been similar to extant squamate eggs. In this case, the water for early embryogenesis would have been provided by sub-embryonic liquid in the oviduct instead of an albumen. Later, an enlarged yolk after absorbing sub-embryonic liquid was shaped into an ellipsoid by the contraction of the oviduct. The authors thus accordingly posited that the elongate eggs would have been at an advanced developmental stage at oviposition because of early embryogenesis from absorbing sub-embryonic liquid in the oviduct (Deeming & Ruta, 2014). Turtle eggs, however, are elongate and are at a later developmental stage at oviposition, thus contradicting to their hypothesis. While the absence of albumen is inconsistent with the phylogenetic bracket, it would be consistent with the absence of chalaza in oviraptorid eggs (see section 7-4-7). Besides, there are few studies or reports regarding preserved yolk in oviraptorid eggs nor in dinosaur eggs. A group of Chinese geneticists claimed that they successfully detected a yolk in an elongate dinosaur egg from the Xixia Basin in Henan, China and successfully extract DNA from the egg (An et al., 1995; Li et al., 1995; Zhang & Fang, 1995), yet these studies were questioned (e.g., Yang, 1995). The claimed dinosaur DNA turned out to be fungal contamination. In addition to the genetic studies, CT scans of an elongate dinosaur egg revealed a round structure that represents a putative yolk (Plate 11 e-h in Mueller-Töwe et al., 2002). The diameter of the round structure is around 2 cm, which is much smaller than Deeming & Ruta (2014)'s suggestion. Eventually, a study of therizinosaurian eggs from China reported an aggregation of embryonic remains in the egg and hypothesized that the aggregation was a result of the confinement of the egg yolk (Kundrát et al., 2008). However, the hypothesis of yolk preservation in dinosaur eggs is pending for more information.

7-4-4 Cuticle in Fossil Dinosaur Eggs?

The cuticle layer has been reported for several fossil dinosaur eggs, but these reports were not verified. Chow (1951) and Young (1954) described a thin and transparent layer in both the innermost and outermost eggshell in an egg from Laiyang, China, and interpreted the outer layer as preserved cuticle. However, Chao & Chiang (1974) reexamined the thin section and suggested that the transparent layer described by Chow (1951) and Young (1954) is simply a calcite layer resulting from recrystallization during diagenesis. Under the polarized light microscope, the cuticle-like layer of dinosaurian eggshells from Laiyang shows columnar cleavage, obvious extinction, and twinkling which is a character for identifying carbonate minerals with low refractive index and high birefringence (Chow, 1951; Young, 1954). Vianey-Liaud et al. (1994) observed a calcite layer overlying eggshell from France and proposed that this layer is a result of the decomposition of the egg's organic material instead of preserved cuticle. However, Kohring & Hirsch (1996) studied the crocodilian and ornithoid eggshells from the middle Eocene of the Geiseltal, Germany, which is famous for its soft-part preservation, and noted the potential preservation of fossilized cuticle and shell membrane. All these previous studies were limited to morphological and histological comparisons between the cuticle on modern avian eggshells and putative cuticle structures on fossilized eggshells.

Recently, cuticle preservation on oviraptorid eggshells was corroborated by chemical analyses using Raman spectroscopy and EPMA (Chapter 3; Yang et al., 2018a). The elemental analysis with EPMA shows high concentration of phosphorus on the boundary between the eggshell and sediment, representing the HAp of the inner cuticle layer. The generally low concentrations of phosphorus in sediments excludes the allochthonous origin of the phosphorus in eggshells, i.e., phosphorus would rather migrate from the egg (including its cuticle) into the sediment than vice versa. The chemometric analysis of Raman spectra collected from fossil and extant eggs provides further supportive evidence for the cuticle preservation on oviraptorid and alvarezsaurid eggshells (Yang et al., 2018a).

A recent taphonomic study concluded that all oviraptorid egg clutches from the Nanxiong Group preserve their clutch architecture and pattern well (He, Huang & Li, 2017). Preservation of eggs or clutches also occurs commonly in the Two Medicine

Formation (Varricchio et al., 1997). The general *in situ* preservation of egg clutches would suggest a relatively high potential of the preservation of soft tissues. Furthermore, a layer of secondary calcite is commonly observed on eggshells from fluvial deposits (Jackson & Varricchio, 2010). The layer of secondary calcite may have been a rigid shield that protected the cuticle layer from mechanical removal if it formed early enough during diagenesis. Based on these observations, Yang et al. (2018a) hypothesized that the *in situ* preservation and the coverage of secondary calcite possibly protected the cuticle layer from being washed away or removed. More detailed microscopic observation of the association between the cuticle and secondary calcite layers will possibly elucidate the taphonomic processes leading to its preservation.

7-4-5 *Membrana Testacea* in Non-avian Dinosaur Eggs?

Although fossil preservation does not favor organic remains, the *membrana testacea* is occasionally preserved in dinosaur eggs as a mineralized layer. *Membrana testacea* preservation has been reported in the eggshells from Auca Mahuevo in Argentina, the Haţeg Basin in Romania, the Tremp Basin in Spain, and Dawa in China (Kohring, 1999; Peitz, 2000; Grellet-Tinner, 2005; Grellet-Tinner, Fiorelli & Salvador, 2012; Reisz et al., 2013). So far, all the fossilized *membrana testacea* was found in sauropod eggs, some of which (Auca Mahuevo) contained embryos, yet no *membrana testacea* has been reported in theropod eggs. Kohring (1999) was the first to summarize the discoveries of fossilized *membrane testacea* and to provide strong evidence of fossilized shell membrane in the dinosaurian *Megaloolithus* sp. eggshells from Spain. Schweitzer et al. (2005a) suggested that organic material such as *membrana testacea* could be preserved in specific taphonomic environments and can be detected by immunological and mass spectrometry evidence. Recently, SEM imaging revealed an enigmatic fiber-like structure near the base of the mammillary layer in the *Triprismatoolithus* eggshell (Yang et al., 2018a). The enigmatic fiber-like structure may be a fiber of the *membrana testacea*. However, fossilized *membrana testacea* in theropod eggs requires more conclusive evidence.

7-4-6 Air Cell in Non-avian Dinosaur Eggs?

Almost all avian eggs have a fixed air cell in the blunt end, but megapode eggs are unique among avian eggs in that the air cell forms anywhere under the shell (Baltin, 1969;

Seymour, 1984; Vleck, Vleck & Seymour, 1984). Ornithological research has revealed that the shell region overlying the cell is more porous than the remainder of the shell. This observation makes fossil eggs amenable to testing for the presence of an air cell because porosity preserves, unlike the air cell. Carpenter (1999a) noted that the elongate shape of theropod eggs was most avian-like among dinosaurs, and suggested that theropod eggs accommodated an air cell in their blunt end as well. Grellet-Tinner et al. (2006) concurred with this, also suggesting the presence of air cell in *Troodon* eggs based on egg shape. In addition, based on a previous phylogeny where *Deinonychus* (Dromaeosauridae) was closer to birds than *Troodon* (Troodontidae), Grellet-Tinner & Makovicky (2006) suggested that the *Deinonychus* egg had an air cell based on the assumption of the existence of an air cell in oviraptorid eggs. However, the latest phylogeny showed that Dromaeosauridae, Troodontidae, and Avialae are in an unresolved trichotomy, thus making the hypothesis of an air cell in the *Deinonychus* egg uncertain. Yang, Cheng & Yang (2011) attempted to infer the existence of an air cell in oviraptorid dinosaur eggs by analyzing the eggshell thickness variation. However, in the embryo-containing egg (NMNS-0015726-F02-embryo-01, Figure 7-11), the eggshell in the blunt end, where the air cell would have been, shows a similar level of internal erosion to any other parts of the egg, thus suggesting that there was no air cell in the blunt end of the egg, protecting the eggshell from calcium removal (Yang, Cheng & Yang, 2011).

On the other hand, Mesozoic bird eggs also present an elongate shape with an acute and a blunt end. Fernández et al. (2013) described a large accumulation of avian eggs from the Late Cretaceous of Patagonia and discussed possible air cells in their blunt end without providing further evidence. In conclusion, to date, an air cell has not been confirmed for any non-avian dinosaur egg, and its presence can only be inferred phylogenetically in fossil Neornithes eggs. Thus, if there was no air cell in oviraptorid eggs, as Yang, Cheng & Yang (2011) suggested, it is very likely that the oviraptorid egg was similar to reptile eggs that have a single-layered shell membrane (see section 7-4-5).

7-4-7 Chalazae in Dinosaur Eggs?

Previous research hypothesized that most reptilian embryos adhere to the shell membrane, and that parental manipulation is harmful or fatal in reptiles (Deeming & Ferguson, 1991), Based on this hypothesis, Varricchio et al. (1997) suggested that *Troodon* eggs lacked chalazae since the partial burial of the eggs precluded parental manipulation (see Varricchio et al., 2013). Varricchio & Jackson (2016) further suggested the absence of chalazae in oviraptorid eggs based on a similar clutch architecture. However, earlier Deeming (2002b) had refuted the hypothesis that the adhesion of a reptilian embryo to the shell membrane is fatal. Therefore, using clutch architecture, and more specifically egg burial (partial or complete), to infer the lack of chalazae appears questionable.

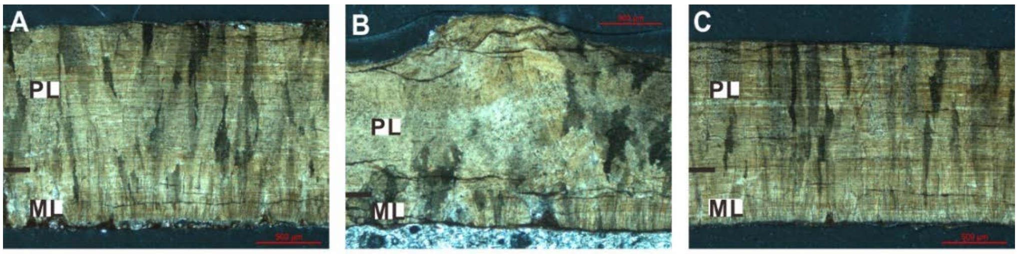


Figure 7-11 Radial sections of eggshells from an embryo-containing egg specimen (NMNS-0015726-F02-embryo-01) attributed to *Heyuannia huangi* from (A) the blunt end, (B) the equatorial region, (C) the acute end in cross-polarized light. Scale bar: 500 μm. Compared to the equatorial region (C), the sections from the blunt (A) and acute (C) ends show a similar microstructure. The erosion in the equatorial region is higher than the others. The similar erosion level at both ends suggests that no air cell existed because the air cell would have protected the inside of the blunt end from erosion. ML, mammillary layer; PL, prismatic layer.

A distinctive feature of oviraptorid and troodontid clutch architecture—the orientation of the eggs, which has never been discussed, may hint for the existence of the chalazae in dinosaur eggs. As reviewed previously, oviraptorid eggs are arranged at an angle >40 degrees to the horizon in the clutch (section 7-3-1 and Chapter 5), and troodontid eggs are nearly vertically arranged (Varricchio et al., 1997). The steep angle of the eggs suggests that the albumen, if present, must have been sufficiently viscous to prevent the yolk from sinking to the bottom of the egg. However, if the albumen was absent in elongate eggs such as oviraptorid and troodontid eggs, as suggested by Deeming & Ruta (2014), there would have been no need for chalaza and they likely were lacking. More evidence is therefore required for verifying aforementioned inferences.

7-4-8 Eggshell Porosity

Eggshell porosity, which controls water vapor conductance, has been extensively studied for investigations of the nesting micro-environments of dinosaurs (Seymour, 1979; Mou, 1992; Deeming, 2006; Jackson et al., 2008; Varricchio et al., 2013; Tanaka, Zelenitsky & Therrien, 2015). The first attempt to investigate the oviraptorid eggshell porosity was done by Mou (1992), who tangentially sectioned several pieces of *Macroolithus yaotunensis* eggshells from the Nanxiong Basin of Guangdong Province, China. The author proposed that oviraptorid clutches were completely buried based on the high porosity comparable to modern buried-nesting crocodile eggshells. On the other hand, the depiction of Norell et al. (1995) and Dong & Currie (1996) showed the oviraptorid eggs at least partially exposed in conjunction with brooding (Figure 7-3 & Figure 7-4; Table 7-1), as discussed above. Later, Deeming (2006) cited Mou (1992)'s porosity data for oviraptorid eggs for the inference that most dinosaur eggs, including those of oviraptorids, were incubated under a substrate cover. However, as noted by Varricchio et al. (2013), the estimation of porosity based on single or several pieces of eggshells is problematic because of the heterogeneous distribution of the porosity in *Troodon* eggs. Yang et al. (2015) and Wiemann et al. (2017) sampled eggshells from four different zones from the blunt end, middle part, to acute end of a *Macroolithus yaotunensis* egg and found that the middle part presents the highest porosity comparable to buried crocodile eggshells, yet the blunt end yields the lowest porosity similar to open-nesting bird eggshells. In combination with the reconstruction of an oviraptorid clutch (see section 7-3-1 and Chapter 5), such a heterogeneous distribution of porosity thus suggests a partially buried (or partially open) nest architecture for oviraptorid dinosaurs (Figure 7-7; Table 7-1; Wiemann et al., 2017). The heterogeneous distribution of eggshell porosity in oviraptorid eggs indicates that the acute end of an oviraptorid egg was buried in a substrate and the blunt end was exposed.

In addition to nesting mode, eggshell porosity is also indicative of incubation period (Massaro & Davis, 2005; Zimmermann & Hipfner, 2007). Ornithologists detected a negative correlation between eggshell porosity and incubation period (Zimmermann & Hipfner, 2007). So far, incubation periods of dinosaurs can be only inferred from histological investigations of embryonic teeth (Erickson et al., 2017). This elegant method, however, is not applicable to oviraptorosaurs because all of them are toothless and have a beaked (except from *Incisivosaurus* for which no embryos in eggs are known).

7-4-9 Pigmentation

The fascinating topic of how the coloration of bird eggs evolved has just now become accessible from a paleontological perspective. In previous views or reconstructions (Figure 7-3 & Figure 7-4; Norell et al., 1995; Dong & Currie, 1996), dinosaur eggs were white like those of modern crocodiles. However, a recent study using chemical analysis found evidence for pigmentation by biliverdin and protoporphyrin in *Macroolithus yaotunensis* eggs from the redbed basins of southeastern China (Chapter 4; Wiemann et al., 2017). The measured and reconstructed absolute and relative abundance of the two pigments suggests that oviraptorid dinosaur eggs were blue-green and visible to parents, conspecifics, and potential predators (Wiemann et al., 2017). The colored eggs have implications for camouflage, mechanical shell strength, and increased bi-parental care as in modern bird eggs. Gosler, Higham & Reynolds (2005) proposed that eggshell can be mechanical reinforced by the inclusion of pigments when eggshell is thinner for a higher water vapor conductance. On the other hand, the water vapor conductance of eggshells in open nests must be reduced to prevent unnecessary water loss. This hypothesis is echoed by the observation that eggshells are thinner at the blunt end (where the air cell is) than at the middle zone in modern bird eggs (Maurer, Portugal & Cassey, 2012), suggesting a trade-off between eggshell thickness/inclusion of pigments (mechanical resistance) and eggshell permeability. In the aspect of geometry, the greater radius of curvature at the blunt end would also have increased stability and thus allow a thinner-shelled blunt end. While the air cell is possibly absent in oviraptorid eggs (see section 7-4-6), the semi-open nesting mode thus requires an exposed blunt end with low water vapor conductance. The inclusion of pigments in oviraptorid eggshells might be a selective advantage for sustaining enough mechanical resistance against brooding adults (inferred from clutch-adult associations, see section 7-5-2 and Chapter 5). In addition to inclusion of pigments, Tanaka et al. (2018) hypothesized that bigger brooding oviraptorosaurs reduced the load on their eggs by enlarging the diameter of the central opening. Yet, the mechanical resistance of eggs against a brooding adult is strongly related to the inclining angle of eggs—a key parameter that was rarely discussed previously.

However, the selective advantages of oviraptorid colored eggshells requires further comparisons with modern birds. Since similar analyses have not yet been performed on *Troodon* eggs, it is not clear if egg coloring evolved in the last common ancestor of oviraptorids and troodontids, i.e., the clade Pennaraptora, or if oviraptorids and modern birds evolved it convergently. The former is suggested by two facts, (1) that therizonosaurs, the sister group to Pennaraptora, have highly porous eggs that were buried and presumably lacked color, (2) that oviraptorid eggs show the same pigments as modern bird eggs.

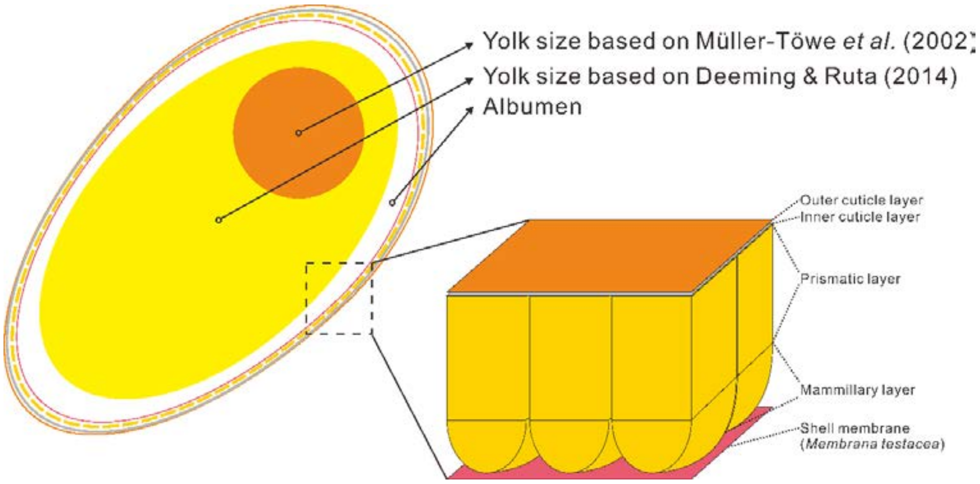


Figure 7-12 Schematic reconstruction of an oviraptorid egg and its eggshell microstructure. Oviraptorid eggs are elongate in shape, with an ornamented blunt end and a smooth acute end. Oviraptorid eggshells have two crystalline layers, including the mammillary layer and prismatic layer but lack the external layer of birds. The eggshell is pigmented by biliverdin and protoporphyrin, coated by the cuticle layer, and underlain by a layer of shell membrane (*membrana testacea*). Note the lack of an air cell and chalazae in our reconstruction. The size of the yolk is still pending for more information. The illustration of a relatively large egg yolk is based on Deeming & Ruta (2014).

7-4-10 The Structure of the Oviraptorid Egg

The variety of studies detailed above allow a comprehensive depiction of an oviraptorid eggs. Macroscopically, an oviraptorid egg is blue-green because of the inclusion of pigments and is elongate, displaying a blunt end, an equatorial part, and an acute end (Figure 7-12). The internal structure of an oviraptorid egg (i.e., yolk and albumen) is unclear despite various surmises. The available evidence suggests the absence of air cell. Microscopically, the oviraptorid eggshell consists of two distinct mineralized crystalline layers including an inner mammillary layer and an outer prismatic layer (Figure 7-12). Chemical evidence indicated the presence of a cuticle layer overlying the mineralized eggshell, yet it is uncertain if the oviraptorid eggshell was underlain by a shell membrane (*membrana testacea*). Represented by a higher porosity in the equatorial part than at both ends, the heterogeneous porosity distribution suggested an at least partially open nesting mode. These various lines of evidence demonstrated a unique egg structure in comparison with all known amniote eggs.

7-5 Inferences on Reproductive Biology

7-5-1 Hatching Asynchrony of Oviraptorid Dinosaurs

Whereas isolated embryo-containing eggs have been reported, such eggs preserved in a clutch could provide much additional information on oviraptorid breeding biology, such as on breeding patterns and hatching hierarchy. Only one partial clutch of embryo-containing eggs has been reported (Weishampel et al., 2008). Yang et al. (2017) report another, better preserved partial clutch with three embryo-containing eggs, a single egg and a pair, from the Late Cretaceous Nanxiong Formation of Jiangxi Province, China (Chapter 5). Based on egg arrangement and geopetal features, there were at least two rings, and the single egg is from the upper ring (see the review of section 7-3-1 and Chapter 5). The single egg thus was laid later than the pair below. This accords with the observation, based on partial preparation of the embryos, that the embryo in the single egg is at an earlier developmental stage than those in the pair, and thus would have hatched later than its putative siblings, an adaptation known as "hatching asynchrony" in extant birds.

The observation of different developmental stages is corroborated by neutron tomographic imaging and differences in eggshell erosion of the single egg vs. the pair (Chapter 5). Hatching asynchrony could have been caused by sequential laying of eggs by a single female or by multiple females contributing to the clutch sequentially. The latter hypothesis is supported by elemental analyses of eggshells from the same clutch that shows inter-pair differences in phosphorus distribution, which is an indicator of female age (Chapter 5). Oviraptorid hatching asynchrony, the only known in nonavian dinosaurs, is inconsistent with the putative brooding behavior because brooding would have synchronized egg development, independently of egg parentage.

7-5-2 Clutch-adult Associations: Brooding? Incubation?

While all archosaurs and many other reptiles lay eggs, this being the plesiomorphic amniote behavior, they show different post-oviposition behavior. Whereas both turtles and crocodiles lay their eggs in a hole they excavate and then bury the eggs in the substrate, turtles abandon the clutch, but some crocodiles show “guarding” behavior to protect eggs from predators. All birds lay eggs and incubate them by direct contact transferring body heat from adults to eggs, except for megapode birds. These incubate their eggs in mounds they built of soil and plant matter, but this peculiar behavior among birds is thought to be secondarily evolved. Some dinosaurs such as *Maiasaura peeblesorum* might have built mound nests, using the heat generated by rotting vegetation for incubation as extant megapode birds and some crocodilians do (Horner & Gorman, 1988; Hechenleitner, Grellet-Tinner & Fiorelli, 2015).

Brooding, a specific behavior of egg-laying animals, especially birds, is initiated by the end of egg-laying and readiness to sit on the eggs (see section 5-1-1 and references therein). Incubation is the process of maintaining uniform temperature, typically elevated above that of the environment, and humidity of the developing eggs, accomplished by one or both parents sitting on the eggs for extended periods of time and by manipulating the eggs (see section 5-1-1 And references therein). An endothermic physiology is generally considered a prerequisite for incubation behavior because endothermy provides metabolic heat to be transferred to the offspring. Oviraptorosaur dinosaurs, like all near-bird dinosaurs, are considered endothermic animals based on bone histological investigations (Erickson, 2005). However, it has been unknown if oviraptorosaurs employed avian brooding or incubation behaviors until the discovery of oviraptorid clutch-adult association specimens.

Evidence for brooding in oviraptorosaurs is seemingly provided by seven spectacular clutch-adult associations specimens: IGM 100/979 in Norell et al. (1995), IVPP V9608 in Dong & Currie (1996), MPC-D 107/15 and MPC-D 107/16 in Fanti, Currie & Badamgarav (2012), AMNH FARB 6517 in Norell et al. (2018), and two undescribed specimens (AGM 4990 of Figure 7-7; Bi & Xu, 2017). In fact, these specimens represent the best evidence for brooding in non-avian dinosaurs. The hypothesis of oviraptor brooding was first proposed by Norell et al. (1995) base on the clutch-adult association IGM 100/979. The authors also suggested that the brooding oviraptor died in a catastrophic sandstorm. Later, in the description of specimen IVPP V9608, Dong & Currie (1996) suggested that the oviraptorid dinosaur was preserved in the laying process; however, the did not provided further supportive evidence. Horner (2000) pointed out that Norell et al. (1995) simply defined "brooding behavior" as the pattern of sitting on the eggs. Deeming (2002a) noted that it was difficult for the adult to sit upon the clutch without disturbing the highly organized egg arrangement. Therefore, if the oviraptorid adult on the clutch had been brooding, the highly organized egg arrangement would have been absent. Deeming (2002a)'s argument, however, was inconsistent with his reconstruction of an oviraptorid clutch (Figure 7-8) and a buried nesting mode inferred by eggshell porosity (Deeming, 2006) because buried or partially-buried eggs (Chapter 4) were unlikely disturbed by a brooding adult. Deeming (2002a) also pointed out that simply using the close physical association of an oviraptorid skeleton with a clutch to infer brooding behavior is insufficient.

On the other hand, there were studies agreeing with Norell et al. (1995)'s hypothesis. For instance, Grellet-Tinner et al. (2006) suggested that the two-layered oviraptorid eggshell was an adaptation to strengthen the eggshell for the lower eggs in a clutch bearing the mass of the upper eggs and the brooding adult. Yet, megapodes eggs are three-layered and not incubated by parents, thus arguing against Grellet-Tinner et al. (2006)'s hypothesis. Moreover, the evidence from the reconstruction of an oviraptorid clutch demonstrated that the long axis of oviraptorid eggs inclined at an angle of >40 degrees to the ground (Figure 7-8; Yang et al., 2018b). Such a high inclining angle of eggs in oviraptorid clutches would have greatly increased the mechanical resistance of eggs against the normal force (i.e., a brooding adult), as suggested by a biomechanical study on dinosaur eggs in different orientations (Zhao & Ma, 1997). In addition to egg orientation, Tanaka et al. (2018) demonstrated that the oviraptorosaurs might have reduced the load on eggs by increasing the diameter of the central opening where accommodate the brooding adult.

Recently, two clutch-adult associations from Mongolia were reported, further supporting the brooding hypothesis and the speculation that the adult suffocated in the sandstorm (Fanti, Currie & Badamgarav, 2012; Norell et al., 2018). However, two unreported clutch-adult associations from the Late Cretaceous fluvial Nanxiong Formation in southern China indicate that the hypothesis of suffocation in a sandstorm cannot explain all clutch-adult associations.

To briefly conclude, the brooding hypothesis is still under debate. Most arguments came from the indistinctive definition of “brooding” and “incubation” (see the clarification in section 5-1-1). Yang et al. (2018b) clearly distinguishes incubation from brooding and suggests that oviraptorids brooded their eggs but did not incubate them (also see section 7-3-1 And Chapter 5). This interpretation is consistent with a low body temperature inferred from a geochemical approach (Eagle et al., 2015, but see Amiot et al., 2017). Based on five complete oviraptorid clutches excavated from Jiangxi Province, China, Yang et al. (2018b) provided a comprehensive reconstruction of an oviraptorid clutch based on all available evidence (Figure 7-8). All eggs were arranged in pairs with their blunt ends pointing inward a center devoid of eggs. The inclination of eggs in an oviraptorid clutch was between 35° and 40°, suggesting a nesting mound. An oviraptorid clutch may consist of up to four rings of eggs. Furthermore, porosity distribution suggests a partially open nest (Yang et al., 2015), supported by the presence of shell pigmentation (Wiemann et al., 2017), with the blunt ends end of the eggs exposed to the air. Yang et al. (2018b) also suggested that the sediment interbedded between the different layers of eggs was part of the original clutch architecture and not added by sedimentary processes after abandonment of the clutch (section 7-3-1).

The multi-ring clutch prevents sufficient heat transfer to the lower rings of eggs, as already noted by Deeming (2002a). Moreover, the sediment separating the eggs and partially encasing them would mean that incubation heat would not easily have reached the lower part of the clutch. Another evidence that contradicts the hypothesis of thermoregulatory contact incubation, in the aspect of clutch arrangement, is the center devoid of eggs. Incubation behavior as a peculiar avian trait is always associated with a brood patch. The brood patch is a feather-less region in an incubating bird’s belly, allowing for efficient heat transfer to the incubated eggs. An incubating bird keeps its eggs close to its body (brooding patch) by building a nest as small as possible, allowing for efficient heat transfer and equal covering of the eggs. The interpretation of incubating oviraptors is inconsistent with the clutch center devoid of eggs right where the brooding patch would have been.

These lines of evidence suggest that the clutch-adult associations are better explained as representing guarding or brooding behavior without thermoregulatory contact incubation as seen in some extant crocodiles. A recent review by Varricchio & Jackson (2016) also noted that these clutch-adult associations suggest a brooding behavior homologous to that in birds, without necessarily implying the thermoregulatory contact incubation. However, Yang et al. (2018b) also suggested that the interpretation of the clutch-adult associations as females preserved during the act of laying eggs may still be valid (Chapter 5) and that the nesting biology of oviraptorids was unique and not analogous to any modern oviparous animals.

Besides, new clutch-adult associations from fluvial deposits of southern China indicated common occurrences in different environments and implied that the adults atop clutch may have been killed by a catastrophic sandstorm or flash flood (see Chapter 5). Hence, although so far is there no consensus on the presence and mode of putative brooding or incubation behaviors in oviraptorid dinosaurs, evidence from various perspectives suggested a distinctive nesting biology in oviraptorid dinosaurs, which is not analogous to any modern oviparous animals.

7-5-3 Parental Care and Polygamy

Parental care is one of the distinctive behaviors that differ birds from other oviparous vertebrates and possibly enables birds to survived the K-Pg extinction event (Varricchio & Jackson, 2016; Tanaka et al., 2018). Parental care consists of pre-hatching care (i.e., guarding, nest construction, communal nesting, brooding, and incubation behaviors) and post-hatching care (parental care and feeding behavior). Previous studies have suggested post-hatching parental care in ornithischian dinosaurs (Horner & Makela, 1979; Meng et al., 2004, but see Zhao et al., 2013), yet there was no tangible evidence of post-hatching parental care in oviraptorid dinosaurs.

Birds have evolved three different parental care strategies, including paternal care, maternal care, and bi-parental care. Among birds, more than 85% of bird species adopt bi-parental care (Whittow & Tazawa, 1991; Wesołowski, 2004). By comparison, paternal care only accounts for less than 1% of all bird species. Interestingly, paternal care is observed in most paleognath birds, such as ostriches and emus. Since birds are surviving dinosaurs, many previous studies have raised the question if any of these mating systems were already present in non-avian dinosaurs (Wesołowski (1994); Burley & Johnson (2002); Wesołowski, 2004).

Using only evidence from living birds, Burley & Johnson (2002) and Wesołowski (1994) proposed female-care first and male-care first models, respectively for the evolution of parental care in birds. Varricchio et al. (2008) compared the ratio of clutch volume to adult body mass in several extant archosaurs with different care systems. They posited that the ratios derived from clutch-adult associations of the oviraptorids *Citipati* and *Oviraptor* and the troodontid *Troodon* are closest to extant paternal-care, polygamous birds because of their high observed clutch volume to adult mass ratio (but see Birchard, Ruta & Deeming, 2013 and Moore & Varricchio, 2016). They also stated that the histological analysis cannot falsify the hypothesis that the supposed brooding oviraptorosaurs were males because none of the skeletons sitting on clutches showed medullary bone, which might give support to Wesołowski's paternal care first model (Wesołowski, 1994).

7-5-4 Communal Nesting

Communal nesting behavior refers to a single clutch being contributed by multiple females, such as in ostriches and emus (van Tyne & Berger, 1961). Communal nesting behavior is observed in all mating systems of birds, including monogamy, polygamy, polyandry, and polygynandry. Varricchio et al. (2008) suggested that the high ratio of clutch size to adult mass indicates communal nesting and polygamy in derived non-avian dinosaurs such as oviraptorosaurs. However, based on a bigger dataset (but megapodes were excluded), Birchard, Ruta & Deeming (2013) considered that the use of the ratio of clutch size to adult mass to infer the communal nesting behavior and polygamy in extinct animals was problematic because they failed to infer the correct mating mode in modern birds using Varricchio et al. (2008)'s methods. Later, the analysis of an even bigger dataset by Moore & Varricchio (2016) concluded that body mass, parental care strategy, and hatchling maturity are significantly correlated to clutch volume across Diapsida, demonstrating the reliability of Varricchio et al. (2008).

Sander et al. (2008) analyzed shell thickness variation in sauropod eggs and found great variation in the eggshells from different clutches of the same nesting horizon but little variation in those from the same clutch. In addition, from a biological perspective, Christians (2002) observed a large variation in egg size of many avian species and pointed out that approximately 70% of the variation in egg size is due to the variation between clutches rather than within a single clutch. These observations also indicate that oviraptorid eggs laid by different individuals would vary in size due to body and pelvis size variation, maternal health, etc., etc. These studies provided possible methods for testing the hypothesis of Varricchio et al. (2008). In addition, Yang et al. (2016) proposed chemical evidence for communal nesting behavior in oviraptorid dinosaurs.

7-5-5 Colonial Nesting

Colonial nesting behaviors is defined as a several to many conspecific birds building their nests and laying their eggs in the same area. The evidence of colonial nesting of dinosaurs in the fossil record has been found in Enantiornithes birds from the Late Cretaceous of Romania (Dyke et al., 2012) and sauropods from France and Spain (Sander et al., 1998; Sander et al., 2008). In oviraptorid dinosaurs, unlike the communal nesting behavior that has been supported by a chemical study (Yang et al., 2016), the colonial nesting was never discussed despite a great number of discoveries of eggs or clutches. Recently, He, Huang & Li (2017) reported a large aggregation of oviraptorid clutches on the same bedding plane, suggesting a possible oviraptorid nesting colony.

7-6 Conclusion

This dissertation aims at comprehensively interpret the reproductive biology of a particular dinosaur group based on all available evidence deduced from the fossil record. The evidence compiled indicates that oviraptorid dinosaurs exhibit many unique reproductive biology traits such as cuticle-coated and pigmented eggshells, highly organized clutches, hatching asynchrony, communal nesting behavior, and polygamy, forming a peculiar group that is not analogous to any modern birds or reptiles. For instance, their spatially highly organized clutches represent a unique reproductive trait not seen in living birds nor reptiles. Their wide distribution and high diversity throughout Asia demonstrate that oviraptorids radiated extensively, possibly based on their innovative egg features and reproductive strategies. Combining traditional paleontological methods with cutting-edge techniques, this dissertation sheds new light on the reproductive biology of oviraptorid dinosaurs, providing new avenues for investigating the reproductive biology of other extinct animals.

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Appendix I (electronic version only)

Raw data of Raman spectrometry of dinosaur and modern eggshells.

Gallus gallus dometicus	*Macroolithus yaotunensis* from Hongcheng Basin, Jiangxi,	*Macroolithus yaotunensis* from Liguanqiao Basin, Henan, China	*Macroolithus yaotunensis* from Nanxiong Basin, Guangdong,	*Triprismatoolithus stepheni* from Sevenhills, Montana, USA	Sediment from Hongcheng Basin, Jiangxi, China	Sediment from Liguanqiao Basin, Henan, China	Sediment from Nanxiong Basin, Guangdong, China	Sediment from Sevenmile Hill outcrops, Montana, USA	*Crocodylia porosus*	*Tomistoma schlegelii*
17416	7271.58	7632.631	3242.95	14595.68	13691.03877	1230.288058	2709.612757	223.526	12601.63955	19309.07633
16849	7198.95	7519	3183.16	14379	13690.24103	1210.486884	2703.389169	196.895	12202.16048	19218.76369
16912	7196.26	7516.947	3212.26	14348.95	13602.444	1189.444	2673.556	181.684	11884	19027.6543
16912	7196.26	7516.947	3212.26	14348.95	13654.17579	1187.392992	2702.723544	181.684	11827.636	19120.55803
17116	7281.79	7562.895	3242.84	14524.53	13671.40112	1175.364564	2732.843655	175.579	11644.56449	19172.86586
17052	7289.95	7535.053	3214.53	14433.95	13625.26859	1161.499601	2737.966241	168.316	11501.66769	19111.36652
16980	7296.58	7595.316	3235.79	14483.21	13723.92373	1160.099786	2776.417451	167.263	11561.12588	19261.48962
17190	7335.21	7609.422	3254.37	14505.58	13889.2351	1158.757385	2799.147449	165.211	11600.93926	19451.16539
16981	7372.63	7613.474	3271.68	14489.89	13953.15253	1158.393967	2789.252652	162	11548.21766	19451.54162
16981	7372.63	7613.474	3271.68	14489.89	13925.334	1162.444	2811.111	162	11549.25	19497.03711
17054	7456.63	7700.263	3280.95	14669.84	13934.65777	1162.444	2814.846255	159.947	11558.15991	19535.21369
17124	7428.84	7725.631	3287.26	14650.63	13966.57626	1166.029975	2836.907876	159	11577.20165	19647.69639
17283	7466.89	7752.105	3289.68	14724.26	14013.77077	1177.238928	2868.695435	163.421	11581.38853	19684.60526
17554	7516.11	7828.421	3345.79	14908.21	14154.06571	1178.804056	2853.510352	161.105	11703.10134	19857.12552
17649	7543.21	7855.79	3342.37	14898.68	14254.74942	1201.8695	2902.387012	161.105	11771.87174	20113.37828
17649	7543.21	7855.79	3342.37	14898.68	14324.111	1196.556	2938.444	161.105	11787.25	20229.69141
17552	7530.74	7899.053	3331.89	14967.42	14311.34359	1197.13858	2934.807664	163.263	11769.80376	20207.49516
17507	7437.26	7795.842	3294.26	14808.53	14181.15609	1202.894743	2900.460043	164.211	11593.81163	19986.76006
17910	7622	7945.842	3379.05	15162.05	14161.7309	1201.395448	2935.5792	171.421	11597.43107	20038.93919
17555	7415.84	7754.737	3277.74	14819.37	14334.69237	1203.104332	2988.476051	177	11775.08132	20270.66546
17555	7415.84	7754.737	3277.74	14819.37	14366.88834	1202.239899	3035.798128	177	11752.96569	20249.85041
18054	7533.79	7877.474	3337.68	15037.63	14263.54937	1198.624402	3014.135414	196.737	11602.07762	20159.62466
17589	7471.68	7812.842	3306.53	14961.47	14111.07266	1199.676923	2980.241575	219.737	11542.9783	20001.43716
17568	7364.26	7713.368	3271.74	14774.26	14099	1199.778	2977.556	242.842	11538.75	19988.82617
17519	7433.95	7796.316	3288.79	14915.16	14185.60881	1192.729688	3010.866681	269.526	11632.14406	20145.41903
17646	7441.58	7813.316	3312	14968.74	14040.67856	1181.757491	2971.016878	281.263	11479.88444	19865.01708
17646	7441.58	7813.316	3312	14968.74	14044.44595	1179.70828	2973.861589	281.263	11506.89034	19933.03467

17483	7391.9	7742.948	3254.26	14807.32	14093.16318	1190.409964	2954.782769	267.947	11425.15389	19943.70291
17368	7418.58	7710.474	3288	14805.95	13988.15557	1208.424456	2948.973225	254.789	11413.09132	19875.66315
17574	7445.21	7775.579	3291.37	14897	13892.02332	1215.98319	2955.090259	248.632	11401.06275	19801.54293
17616	7451.68	7777.369	3289.95	14869.58	13870.223	1217	2957.333	236.158	11395	19781.62109
17549	7355.21	7725.895	3257.74	14691.68	14078.1963	1240.1164	2971.593135	216.211	11469.9439	20040.74932
17549	7355.21	7725.895	3257.74	14691.68	14152.83949	1239.270521	2980.676316	216.211	11489.80799	20095.35462
17486	7343.16	7645.421	3254.16	14592	14199.45439	1244.488584	2999.454566	195.947	11509.97547	20149.18508
17508	7319.05	7638.737	3250.11	14601.26	14261.46442	1265.69095	3017.398712	174.053	11569.21146	20266.1435
17333	7115.26	7485.421	3183	14357.42	14317.91081	1271.942313	3023.965616	162.316	11621.47231	20358.36956
17312	7056.32	7584.053	3182.79	14459.68	14389.10911	1289.623394	3061.744494	152.158	11712.37012	20535.71105
17356	7032.1	7569.369	3161.95	14426.05	14424.444	1307.111	3093.222	146.632	11775	20655.07031
17356	7032.1	7569.369	3161.95	14426.05	14419.35811	1317.336755	3088.992348	146.632	11710.11	20571.5613
17205	6925.79	7533.736	3138.79	14409.47	14432.46125	1337.922093	3103.723477	139.421	11721.64183	20552.31716
17184	7022.21	7590.631	3142.95	14549.21	14480.6437	1366.973001	3137.406315	140.842	11810.86976	20652.39799
16793	6906.84	7427.632	3062.53	14309.58	14533.97435	1399.288742	3144.773443	136.842	11790.87741	20695.14236
17058	6961.47	7448.737	3065.89	14361.47	14651.16563	1429.796534	3161.305937	135.737	11844.90317	20875.38036
16916	7022.79	7461.421	3079.42	14396.32	14802.556	1459.222	3206.667	134.737	11958	21123.93359
16916	7022.79	7461.421	3079.42	14396.32	14745.13087	1447.175074	3196.727203	134.737	11943.15594	21069.40338
16926	7076.05	7420.525	3092.32	14396.68	14625.72244	1417.429887	3172.917343	134.053	11882.42129	20949.70826
16699	7059.11	7378.947	3083.95	14346.79	14635.00329	1403.006099	3169.045924	129.579	11831.02382	20967.62563
17031	7227.26	7456.895	3134.47	14472.63	14621.93353	1376.195638	3172.178188	135.368	11881.73812	21006.99755
16994	7186.47	7444.421	3133.42	14390.42	14588.99611	1339.491824	3163.00351	132.579	11875.98553	20932.48242
16875	7219.11	7447.895	3158.42	14361.89	14536.67053	1338.623818	3152.904796	137.474	11879.26189	20929.35381
16875	7219.11	7447.895	3158.42	14361.89	14559.333	1301.889	3149.889	137.474	11759.75	20918.51758
17038	7261.68	7461.79	3147.16	14414.26	14549.26214	1300.953705	3151.501948	132.632	11771.78018	20923.71368
17043	7346	7527.263	3210.26	14563.26	14476.63072	1294.074723	3162.469043	133.842	11853.59458	20954.17311
17239	7341.84	7514.632	3203.53	14569.58	14477.36229	1292.257028	3157.749287	133.947	11806.96792	20896.16237
17417	7439.95	7621.21	3228.84	14723.53	14512.26142	1286.916433	3179.424274	135.368	11816.44155	21030.96452
17776	7506.58	7748.263	3286.79	15006.74	14635.11763	1295.399152	3227.417768	138.632	11885.65613	21195.47903
17776	7506.58	7748.263	3286.79	15006.74	14325.4882	1264.295758	3170.503417	138.632	11602.28442	20721.6543
18164	7565.47	7894.79	3305.32	15176.42	14781.53876	1320.087411	3285.574097	140.368	12033.95839	21404.61755
18693	7701.79	8082.895	3393.26	15493.53	14802.667	1322.667	3290.889	138.105	12054	21436.3457
18857	7781.74	8207.21	3422.79	15717.53	14425.16926	1281.123427	3216.911331	142.105	11750.00592	20941.29099
19046	7759.84	8214.789	3412.53	15700.58	14699.27929	1304.586597	3324.683657	143.632	12043.37815	21368.11083
19063	7849.95	8283.315	3468.74	15837.11	14722.85927	1302.183497	3380.549195	146.737	11982.37263	21331.92962
19063	7849.95	8283.315	3468.74	15837.11	14643.51417	1306.454101	3481.381489	146.737	11916.08647	21255.39963
18791	7819.63	8218.63	3417.32	15818.26	14859.05403	1335.84511	3778.478249	143.263	12101.66384	21555.19365

19109	7831.9	8216.842	3435.32	15753.58	14769.84098	1338.926698	4118.760515	144.526	12042.61774	21543.25259
19353	7959.63	8344.789	3466.16	15989.63	14836.21208	1353.721746	4369.150785	148.053	12105.70195	21631.46974
19040	7847.16	8284.737	3450.32	15844.42	14877.111	1359.556	4429.556	146.579	12141	21674.03516
19533	7905.9	8313.526	3476.68	15949.68	14957.81252	1351.779906	4443.899478	148.053	12173.43309	21806.52954
19533	7905.9	8313.526	3476.68	15949.68	14907.51613	1349.704978	4336.723331	148.053	12168.22027	21787.8826
19739	8003.74	8448.158	3498	16144.79	14907.49249	1359.363537	4171.446255	148.632	12166.76376	21794.80007
19409	7831.68	8273.632	3420.74	15843.26	15018.03285	1351.274403	3968.79863	141.053	12270.60178	21943.85459
19563	7986.53	8402.157	3490.42	16104.89	15066.85303	1336.278729	3784.231901	147.526	12315.95167	22047.57001
19377	7858.37	8326.685	3429.63	15965.26	14999.05199	1329.552899	3647.260561	142.947	12253.20442	22013.71429
19500	7904.58	8392.842	3459.79	16080.42	14945.889	1327.667	3589	143.211	12213.5	21969.96484
19500	7904.58	8392.842	3459.79	16080.42	15025.07329	1334.414182	3576.045352	143.211	12276.62999	22079.91688
19647	7924.1	8366.737	3484.84	16091.37	15070.48937	1342.370488	3538.855407	146.316	12329.6417	22139.16274
19599	7858.74	8334.579	3433.16	16026.68	15006.8374	1343.667964	3471.165934	146.105	12268.5049	22026.52977
19756	7843.47	8332.211	3421.68	15965.53	14980.38425	1346.931442	3415.378386	142.632	12209.35069	21988.03984
19733	7900.32	8364.21	3441.11	16103.05	14923.40957	1346.610408	3392.87274	144.263	12174.73106	21967.26254
19702	7864.21	8296.105	3432.05	15975.16	14900.09143	1340.57887	3375.955706	144.211	12164.42758	21973.35823
19669	7862.79	8347.843	3428.26	16077.37	15023.889	1343.333	3400.889	145.263	12254	22147.6543
19669	7862.79	8347.843	3428.26	16077.37	14957.70209	1342.262001	3389.203252	145.263	12203.41038	22053.11643
19545	7870.53	8298.79	3429.68	16027.79	14841.90763	1339.196188	3367.891338	144.368	12116.59164	21887.36369
19662	7901.58	8337.21	3434.47	16077.47	14973.95429	1343.51915	3395.304665	145	12224.76866	22085.1101
19669	7811.32	8272.632	3412.79	15946.26	14984.69502	1360.039546	3414.86242	147.053	12244.66868	22138.21111
19700	7883.16	8358.211	3436.21	16056.74	14926.28954	1354.130981	3397.89951	146.579	12200.77454	22073.20748
19751	7850.79	8329.421	3427.26	16042.79	14921.92106	1353.528356	3419.601721	148.842	12130.65455	22039.01614
19751	7850.79	8329.421	3427.26	16042.79	14873.00277	1344.755165	3384.317717	148.842	12130.86583	22038.79673
19475	7798.47	8209.579	3412.53	15796	15036	1348.444	3383.444	150.105	12183.75	22272.51758
19686	7855.95	8343.633	3417.32	16059.84	15022.09432	1348.608937	3382.446815	152.526	12182.00494	22257.37334
19868	7982.42	8429.579	3488	16228.32	14840.31783	1350.898592	3368.324942	160.684	12156.84911	22059.64491
19442	7790.95	8256.21	3382.21	15865.21	14869.4953	1353.452511	3347.205444	174.526	12111.60873	22108.11428
20082	7975.05	8445.526	3467.74	16200	15180.52924	1347.080204	3414.595806	196.368	12274.92415	22473.52724
20082	7975.05	8445.526	3467.74	16200	15008.34878	1352.869745	3379.371629	196.368	12227.07199	22306.50307
19944	7903.37	8376.737	3436.32	16070.53	15181.19137	1353.836499	3402.756451	217.421	12225.23307	22369.75071
19792	7845.26	8348.104	3435.05	15997.9	14939.64571	1339.109375	3374.492725	226.789	12177.07046	22278.92302
20252	8017.9	8494.633	3510.53	16312.9	14912.889	1337.556	3371.333	232.684	12172	22268.82617
20176	7932.53	8421.158	3457.9	16102.16	15121.42923	1354.170805	3410.13373	225.526	12281.57338	22517.73201
20152	7983.47	8473.369	3488.32	16296.68	15174.85754	1370.805039	3368.706474	218.842	12345.97831	22589.85083
20133	7982	8443.157	3471.16	16167.37	15233.16377	1370.60074	3402.173834	205.105	12437.33679	22673.41645
20133	7982	8443.157	3471.16	16167.37	15340.53873	1368.755126	3428.635103	205.105	12475.55557	22812.04074

20290	7970.79	8444.736	3444.47	16198.84	15344.83816	1375.175517	3435.849006	199.421	12491.27588	22901.47497
20538	8062.11	8578.895	3509.32	16444.89	15248.35585	1372.259557	3411.957638	186.316	12355.43322	22730.51238
20438	8031.84	8543.842	3506.53	16344.26	15301.29427	1377.47781	3411.002163	170.737	12399.70521	22807.29842
20620	8021.21	8507.946	3475.47	16333.53	15342.333	1380.889	3415.222	164.789	12446.5	22878.62695
20697	8019.79	8561.685	3499.47	16380.16	15316.16158	1384.866814	3397.984178	155.211	12444.61627	22889.23152
20697	8019.79	8561.685	3499.47	16380.16	15277.84321	1379.747743	3413.2712	155.211	12408.97583	22878.91142
20508	7977	8495.475	3470.16	16340.95	15317.46917	1382.861325	3454.663302	155.526	12436.09689	22927.58398
20471	7991.63	8475.21	3474	16377.68	15277.85895	1375.799813	3424.895314	153.895	12479.22299	22908.55352
20680	8049.47	8523.896	3505.58	16442.26	15377.09345	1384.44888	3435.801745	156.105	12567.84416	23104.57184
20682	8075.31	8568.474	3520.58	16486.16	15307.77391	1396.67855	3422.470322	157.789	12494.32403	23063.20106
20422	7954.63	8447.21	3444.26	16240.84	15209.53982	1403.086245	3399.974207	161.105	12443.24526	22947.21092
20569	7936.26	8448.736	3442.1	16280.63	15366.667	1417.778	3447.333	174.684	12567.75	23144.0332
20569	7936.26	8448.736	3442.1	16280.63	15324.29058	1404.753128	3435.800697	174.684	12437.46958	23044.77272
20822	7970.32	8559.632	3470.32	16424.68	15219.61643	1390.497291	3402.818869	176.053	12318.9272	22911.46727
20765	8001.79	8503.896	3480.05	16346.42	15192.69945	1401.191414	3388.092864	178.684	12454.53817	22975.2738
20784	8001.95	8471.842	3467.16	16319.11	15237.66857	1408.681228	3397.224522	179.947	12452.4315	22995.19954
20511	7879.74	8376.632	3435.05	16211.95	15161.82259	1414.074478	3367.805731	175.737	12344.45146	22870.03119
21001	7971.16	8520.736	3459.16	16373	15138.64124	1416.709747	3359.595018	172.842	12258.51431	22863.26891
20608	7916.84	8398.316	3429.42	16216.05	15104.67501	1416.355897	3363.668708	166.053	12240.00282	22802.22694
20608	7916.84	8398.316	3429.42	16216.05	15140.777	1416.778	3381.889	166.053	12265.25	22812.06836
20710	7904.32	8439.264	3445.16	16262.47	15139.91138	1423.599492	3377.829083	157.684	12282.0671	22831.40491
20728	7871.58	8463.527	3432.63	16269	15120.51158	1455.696545	3360.33336	152.105	12338.16603	22898.24811
20778	7856.42	8360.789	3404.21	16114.95	15058.21312	1467.849007	3360.070704	141.579	12248.16505	22813.80722
20669	7845.05	8325.632	3393.74	16059.05	15193.01563	1473.439184	3346.911466	143.895	12289.15304	22902.5856
20924	7948.05	8486.686	3458.68	16295.79	15152.16813	1478.368105	3349.797876	144.158	12339.91865	22943.25582
20924	7948.05	8486.686	3458.68	16295.79	15150.52674	1467.404409	3335.473041	144.158	12273.98537	22895.84873
20854	7864.26	8402	3406.16	16179.89	15160.1884	1460.171925	3347.456682	138.789	12278.76958	22948.2105
21073	7909.47	8449.473	3424.95	16219.26	15224.14764	1474.10883	3359.017127	142.526	12279.7417	23030.30111
20969	7928	8457.474	3429.37	16309.47	15224.667	1474.222	3359.111	139.263	12279.75	23031.00195
21030	7955.79	8464.475	3426.68	16261.26	15215.92698	1465.481981	3340.485666	140.474	12312.28735	23048.11003
21197	7991.53	8537.421	3498.37	16355.63	15217.96067	1468.12211	3355.688495	139.737	12381.98114	23123.988
21230	7924.42	8492.736	3438.89	16238.74	15058.03653	1448.959564	3316.699273	141.263	12302.63689	22929.98689
21230	7924.42	8492.736	3438.89	16238.74	15358.24872	1512.534116	3377.991608	141.263	12506.28602	23389.05831
21493	7995.53	8517.263	3453.53	16361.47	15387.84133	1507.096013	3375.954606	141.105	12478.85487	23406.41811
21378	7955.84	8538.684	3446	16319.47	15502.81729	1495.48316	3395.198743	142.053	12570.59773	23534.34458
21363	8035.63	8545.843	3477.58	16396.31	15455.03672	1518.621052	3372.432525	141.632	12632.69756	23548.53341
22011	8172.95	8694.896	3537.32	16643.89	15431.777	1526.111	3364	141.105	12643.25	23542.07031

21781	8057.79	8663.473	3497.53	16536.31	15423.43033	1511.722191	3388.087715	137.737	12554.02566	23526.89972
21712	8073.84	8658.79	3501.26	16562.9	15484.57806	1540.983677	3402.631769	143.263	12616.96157	23703.36179
21712	8073.84	8658.79	3501.26	16562.9	15579.45707	1547.060967	3390.953906	143.263	12639.48002	23726.17135
22172	8186.47	8714.369	3557.84	16637.21	15704.32927	1550.640305	3404.781017	139.684	12695.77844	23887.47238
22104	8112.26	8699.421	3517.16	16643.37	15677.05898	1556.943264	3411.625908	146.789	12712.27987	23952.31195
22086	8135.1	8713.052	3511.63	16693.21	15653.58797	1556.111664	3413.622771	138.474	12740.49446	23936.41953
22187	8127.89	8733.053	3526.42	16686.32	15654.74775	1554.339671	3413.088891	140.421	12707.59311	23950.89636
22348	8143.79	8702.631	3497.16	16762.68	15610.51421	1535.687241	3414.086253	138.737	12667.67074	23958.99033
22346	8110.53	8671.948	3531.26	16697.63	15585.111	1519	3418.444	139.579	12679.75	23963.79102
22346	8110.53	8671.948	3531.26	16697.63	15602.99167	1518.637097	3399.008636	139.579	12659.23547	23947.34515
22368	8156.63	8702.525	3522.21	16766.69	15602.43983	1513.641154	3379.896958	141.895	12665.88691	23899.55618
22675	8194.42	8762.315	3538.26	16880.63	15546.26856	1501.609886	3381.238767	144.368	12690.22243	23856.63933
22096	7964.63	8548.631	3447.11	16486.32	15571.73205	1493.246257	3388.258733	141	12718.10135	23960.11362
22936	8204	8786.685	3557	16922.9	15498.73428	1463.686134	3365.432886	143.368	12635.85115	23871.80873
22295	7969.11	8581.368	3436.58	16508.95	15346.46846	1433.227568	3322.179805	140.211	12502.09614	23671.08195
22990	8143.84	8720.157	3538.21	16822.84	15637.20386	1469.618783	3376.248719	138.421	12752.97243	24137.19537
22620	8049.79	8657.315	3499.74	16642.37	15472	1437.667	3360.778	143.684	12588.5	23855.55273
22620	8049.79	8657.315	3499.74	16642.37	15427.58821	1433.909141	3343.786519	143.684	12561.27231	23795.94436
22546	7997.32	8578.947	3444.42	16498.69	15308.72821	1420.207062	3296.662627	138.632	12507.231	23660.2292
22891	8064	8655	3492.89	16726.74	15377.14401	1408.723769	3313.780771	141.842	12594.23001	23800.59418
22606	7994.79	8572.157	3456.58	16531.84	15408.74426	1396.802422	3312.109425	138.895	12515.58157	23692.22311
22741	8005.84	8606.368	3460	16542.05	15443.82737	1414.805235	3332.633721	138.632	12566.64577	23831.59113
23070	8056.68	8638.685	3474.74	16650.9	15193.84711	1385.695259	3283.607734	138.211	12538.32184	23612.46228
22819	7993.1	8567.21	3461.89	16514.26	15467.5288	1416.745927	3284.645728	139.316	12719.05383	23935.75159
22819	7993.1	8567.21	3461.89	16514.26	15375.7823	1416.435745	3302.014453	139.316	12801.19781	23882.652
23182	7999.74	8589.843	3447.63	16477.05	15435.444	1393.667	3292	138.526	13009	24023.38477
23252	8074.26	8687.158	3504.32	16653.63	15435.444	1393.667	3292	138.263	13009	24023.38477
23689	8050.84	8687.526	3501.58	16619.73	15438.45775	1400.230046	3251.218471	137.842	13566.72227	24088.688
23587	8059.11	8625.105	3485	16599.27	15540.43348	1393.54797	3293.35665	134.263	14615.4252	24408.64468
23986	8140.68	8733.264	3533.89	16739.37	15389.52282	1376.370286	3227.625015	139.789	15432.9745	24278.00859
23833	8066.37	8717.368	3491.63	16733.89	15628.59732	1406.151675	3272.155625	140.053	15774.01412	24764.65744
23833	8066.37	8717.368	3491.63	16733.89	15538.21144	1378.767117	3277.062248	140.053	15037.01782	24519.60028
23932	8087.95	8706.578	3488.42	16634.11	15578.26937	1400.297463	3271.060728	139.316	14386.70191	24536.75601
23877	8112.32	8713.104	3535.58	16714.26	15635.59518	1381.174207	3287.806517	142.158	13844.737	24505.85813
23910	8103.11	8654.369	3489.21	16677.32	15649.7653	1377.004063	3273.202296	142.105	13411.34239	24444.16316
24426	8186.95	8808.314	3498.26	16894.16	15650.667	1377.555	3267.667	140.737	13316.25	24429.41211
24287	8067.89	8701	3485.74	16673.58	15754.74203	1395.541118	3286.61138	140.579	13210.87518	24659.8816

24358	8201	8801.578	3516.11	16838.79	15601.43509	1390.336267	3239.819417	140.737	12961.63929	24466.02153
24611	8209	8826.947	3541.05	16939.11	15723.32737	1388.283559	3237.0678	141.158	12923.85437	24576.58909
24611	8209	8826.947	3541.05	16939.11	15818.13493	1388.727703	3257.643063	141.158	12949.36491	24709.84968
24652	8121.21	8804.736	3522.05	16866.63	15704.76515	1367.166868	3239.142328	139.579	12894.14474	24638.92038
24546	8121.47	8807.842	3502.26	16916.11	15681.47464	1357.779818	3227.926738	141.684	12781.69295	24556.27224
24548	8080.53	8733.79	3487	16763.05	15824.73006	1368.719924	3255.098466	143.421	12858.81155	24753.64983
24671	8161.79	8796.053	3526.21	16997.68	15779.20045	1363.486815	3245.246676	140.842	12845.94925	24714.57882
24681	8092.16	8746.895	3476.58	16789.58	15613.06571	1356.873215	3217.615605	138.526	12734.38662	24479.73946
24781	8061.89	8734.579	3463.21	16800.21	15568.111	1360.889	3216.444	141.368	12731.75	24440.92969
24781	8061.89	8734.579	3463.21	16800.21	15620.97237	1365.953636	3209.068325	141.368	12719.25186	24497.91096
25011	8153.63	8808.841	3514.26	16975.31	15606.60099	1369.242594	3187.046475	142.947	12696.65378	24500.76357
24677	8073.32	8699.264	3488.42	16791.26	15524.21474	1363.727595	3172.509271	135.737	12682.25879	24411.51126
24642	8009.42	8699.526	3467.11	16747.16	15653.57633	1362.688148	3184.082937	138.737	12741.71585	24543.34135
24809	7991.21	8607.947	3434.37	16599.58	15663.38703	1351.978895	3170.661929	138.368	12734.71899	24553.53416
25108	8019.9	8684.158	3462.74	16751.26	15397.04829	1331.715687	3116.573886	143.789	12534.77322	24213.54178
24914	8039.47	8642.684	3447.53	16696.47	15355.96991	1339.193416	3105.935862	139	12612.66887	24287.62064
25110	7961.68	8643.104	3441.26	16632.16	15282.91274	1334.63604	3092.66866	136.895	12473.14379	24087.32264
25110	7961.68	8643.104	3441.26	16632.16	15349.333	1336.889	3048.778	136.895	12422.25	24113.07031
25312	8027.63	8700.316	3440.58	16704.95	15370.53939	1342.486671	3056.916122	141.474	12447.00854	24156.81786
25237	8002.53	8642.263	3452.79	16693.63	15429.13023	1360.295364	3077.32062	145.211	12514.24179	24274.18375
24994	7890.95	8536.315	3399.53	16484.63	15282.06794	1333.46888	3014.69085	137.526	12343.94904	23965.13489
25459	7939.16	8628	3432.26	16580.79	15307.32956	1339.429069	3043.213745	140.737	12425.56537	24103.66721
25301	7956.53	8603.054	3432.21	16584.32	15409.62111	1350.724044	3023.689818	145	12526.47815	24288.08231
25310	7944.95	8621.79	3434.95	16532.37	15269.79032	1329.658028	2997.343518	147.421	12335.13261	23996.60003
25545	8002.84	8642.686	3445.47	16561.37	15424.38963	1336.945254	3024.465304	143.579	12524.64841	24294.5798
25545	8002.84	8642.686	3445.47	16561.37	15176.111	1331.111	2970.444	143.579	12334.03638	24006.91428
25543	7939.95	8594.001	3397.89	16493.79	15438.32766	1329.166249	2994.754365	150.579	12484.95341	24289.57228
26285	8141.68	8811.684	3496.89	16867.31	15404.73417	1347.165727	3028.404725	149.526	12469.41675	24352.8855
25445	7931	8623.475	3408.32	16542.9	15402.333	1348.222	3030.333	151.316	12468.25	24356.13672
26198	8084.26	8752.158	3497.16	16823.69	15525.42557	1355.334865	3024.010552	151.053	12513.81465	24408.4093
26228	8009.1	8736.211	3452.53	16672.58	15691.30934	1369.91552	3059.035955	163.158	12707.10831	24668.91669
26290	8067.26	8724.579	3478.11	16723.69	15419.51727	1348.206749	2974.442664	159.842	12475.2622	24316.6514
26648	8149.79	8840.317	3512	16922.47	15475.0874	1343.175418	3004.12099	167.737	12532.84511	24478.62561
26648	8149.79	8840.317	3512	16922.47	15694.26657	1341.90026	3013.479445	167.737	12618.40219	24748.81047
26757	8126.37	8790.105	3485.68	16854.79	15751.53087	1371.678823	3016.059665	170.421	12731.91918	24899.07318
26911	8176.89	8857.104	3518.84	16940.26	15659.97845	1357.866946	2989.532057	179	12724.57803	24747.62732
27038	8139.74	8869.524	3507.79	16920.16	15680.55772	1339.810633	2967.249682	185.789	12754.35682	24827.37493

27142	8151.84	8880.842	3490.53	17002	15719.84682	1347.172772	2969.089447	201.211	12775.00195	24852.20916
27488	8237.63	8956.632	3524.47	17128	15727.222	1352.778	2972.556	217.789	12775.5	24832.10547
27651	8251.74	8913.474	3538.05	17059.9	15739.684	1362.515813	2969.150922	238.053	12768.7615	24873.57021
27658	8246.16	8979.946	3544.16	17181.58	15799.15171	1368.861754	2957.902134	279.579	12810.39946	24957.29634
27658	8246.16	8979.946	3544.16	17181.58	15889.60135	1364.540466	2965.256292	279.579	12882.00518	25095.95852
27883	8248.05	8960.104	3546.84	17177.89	15965.87453	1369.826801	2963.511661	332	12930.46797	25227.40843
27793	8241.16	8944.053	3542.95	17139.79	15880.10123	1369.300613	2928.071569	426.368	12877.49846	25166.20435
27932	8203.58	8941.79	3511.84	17162.16	15821.01787	1359.734412	2921.03628	523.632	12829.42283	25119.14425
28017	8216.11	8926.632	3546.32	17152.05	15877.84038	1354.511272	2935.955825	589	12835.42712	25162.95345
28188	8205.05	8970.896	3524	17164.95	15764.75686	1346.471718	2904.166984	596.211	12747.93962	24967.85749
28188	8224.95	8924.105	3538.63	17119.31	15714.96296	1351.452365	2879.838341	563.579	12728.558	24880.99975
27932	8073.16	8812.314	3499.89	16954.37	15819.57662	1359.662508	2889.538978	529.737	12828.70588	25043.12891
28623	8270.63	8981	3546.42	17310.84	15733.556	1348	2870.667	529.526	12801.5	24938.34375
28623	8270.63	8981	3546.42	17310.84	15792.92649	1346.15002	2873.578869	529.526	12812.90455	25006.7283
28318	8161	8960.895	3500.84	17136.47	15863.85276	1341.282827	2868.887638	507.211	12792.45306	25071.07509
28480	8151.21	8928.106	3498.58	17176	15689.96714	1335.001538	2832.125704	488.421	12655.79144	24816.50272
28301	8147.1	8866.685	3497.68	17036.74	15670.67312	1322.740317	2812.31144	429.79	12603.27475	24784.89669
28251	8085.58	8869.105	3494.58	17035.1	15728.87816	1327.775787	2817.401536	375.316	12600.03026	24897.46794
28723	8152.05	8861.578	3498.1	17057.68	15664.88024	1337.108221	2792.605368	326.579	12591.39371	24780.71788
28456	8093.16	8846.001	3489.95	16992.63	15754.65659	1339.765113	2818.877674	281.632	12741.19972	25004.48465
28693	8180.53	8940.578	3503.37	17114.26	15739.76558	1330.715983	2771.061845	245.947	12666.25736	24869.12358
28693	8180.53	8940.578	3503.37	17114.26	15476.31299	1313.57419	2752.774318	245.947	12593.12501	24679.28196
28843	8124.95	8881.789	3495.42	17021.11	15696.889	1318.444	2744.556	213.263	12615.5	24869.20898
28622	8106.32	8840.054	3471.11	16992.58	15700.33721	1318.977197	2745.34877	192.474	12618.00887	24870.58341
28618	8147.26	8897.315	3476.21	17011.69	15805.23808	1335.32028	2769.539349	174.684	12695.06158	24912.27532
28903	8140.95	8887.158	3489.89	16991.63	15590.23753	1332.187321	2738.098906	166.737	12584.96949	24721.47104
29140	8139.32	8901.578	3496.26	17065.84	15824.28338	1329.580823	2737.75517	162.789	12727.13295	25040.52326
28982	8173.95	8906.685	3504.26	17057.32	15729.86637	1330.365073	2753.845204	162.632	12743.05882	25014.30889
29147	8147.11	8904.21	3501.37	17045.11	15628.54691	1336.897079	2702.610154	160.895	12665.825	24873.50542
29478	8233.32	9018.79	3535.11	17250.37	15644.68575	1345.939956	2714.611427	160.105	12672.73063	24856.89413
29478	8233.32	9018.79	3535.11	17250.37	15748.03008	1324.881069	2721.168047	160.105	12768.65903	25050.03614
28775	8017.53	8767.264	3423.42	16778.37	15656.81407	1324.067902	2679.742928	155.211	12675.94702	24950.71002
29880	8322.37	9083.686	3554.58	17365.79	15786.20692	1331.932015	2691.104909	156.105	12757.77217	25076.7277
29527	8171.53	9000.948	3509.05	17152.84	15726.66212	1328.688267	2674.93935	153	12730.56743	25024.7389
29232	8146.21	8874.263	3490.47	17065.11	15693.333	1327	2667.778	154.158	12712	24993.58398
29691	8208.42	8998.368	3515.68	17169.32	15859.7809	1342.548384	2684.803418	150.842	12845.08205	25212.26601
29705	8201.21	9007.577	3522.53	17179.63	15763.58944	1331.891471	2670.745846	146.053	12760.45341	25103.27813

29940	8283.58	9068.579	3545.89	17342.1	15732.37022	1335.903875	2671.216874	157	12707.51447	25058.7252
29786	8184.84	8983.421	3511	17155.53	15780.0282	1335.307798	2670.848488	149	12770.765	25137.07283
29786	8184.84	8983.421	3511	17155.53	15773.0915	1333.480772	2643.393387	149	12799.78989	25159.51713
30223	8324.11	9102.315	3585.84	17427.37	15862.12075	1348.734506	2633.988648	157.421	12811.09312	25247.74225
30161	8284.74	9057.368	3580.58	17373.89	15983.4313	1350.099979	2641.223301	159.684	12827.3005	25419.19171
30179	8280.63	9071.315	3565.68	17441.63	15765.42746	1309.211892	2620.396396	167.789	12701.73673	25135.96803
30216	8260.58	9060.104	3541.37	17340.53	15730.44463	1310.16164	2606.633449	174.789	12706.57371	25086.6944
30342	8289.21	9110.632	3569.21	17367.95	15984.2091	1341.37562	2619.550513	174.842	12845.97001	25415.16845
30114	8167.9	9023.105	3520.84	17238.37	15949.34369	1327.668179	2606.498746	174.263	12840.11545	25367.24373
30560	8359.16	9179.264	3611.89	17560.79	15866.223	1317.222	2581.889	179.368	12839.25	25321.10352
30455	8230.95	9058.789	3548.16	17364.21	15881.62932	1319.265485	2587.160648	173.263	12841.73172	25325.54059
30455	8230.95	9058.789	3548.16	17364.21	15912.83239	1324.628487	2590.254825	173.263	12848.80317	25342.85023
30552	8267	9083.211	3578.95	17393.95	15865.15109	1326.589867	2571.790915	172.947	12792.41699	25277.84415
30616	8232.9	9083.789	3569.37	17349.47	15821.01166	1325.402575	2556.161105	173.474	12723.01374	25194.77747
30743	8255.58	9112.264	3548.42	17359.74	16005.31133	1333.842908	2557.145012	169.316	12883.22835	25457.00975
30827	8336.47	9177.158	3590.58	17514.52	15905.03555	1337.516925	2559.437898	165.579	12820.55532	25414.54435
30524	8244.74	9011.791	3553.37	17250.79	15766.30302	1323.664644	2538.007099	157.316	12685.905	25203.0405
30822	8313.68	9126.157	3581.05	17481.27	15825.33016	1313.285936	2506.581069	155.842	12704.73018	25204.57917
31057	8318.79	9174.895	3597.95	17499.37	15861.92548	1315.632635	2496.725227	154.579	12771.55493	25236.34742
30762	8255.58	9102.053	3547.68	17446.31	15801.63803	1301.750732	2516.753979	137.947	12711.25827	25149.78248
30762	8255.58	9102.053	3547.68	17446.31	15816.95578	1316.011801	2504.647445	137.947	12719.80003	25075.18676
30705	8247.69	9068.106	3573.26	17327.79	15988.223	1320.556	2508.889	145.474	12860.5	25390.58789
31216	8395.42	9239.157	3607.42	17564.1	15982.26165	1320.240165	2507.341412	145.421	12856.31185	25385.50973
30857	8284.63	9056.475	3584.68	17354.05	15820.3593	1311.620036	2465.205931	131.474	12742.27973	25246.88502
30547	8268.1	9102.842	3568.74	17370.89	15810.42468	1306.111819	2450.302545	141.842	12745.92516	25207.16118
30614	8327.37	9172.842	3594	17478.74	15755.60411	1280.490098	2459.420697	141.421	12656.45992	25065.2691
30865	8279.63	9120.001	3594.42	17358.32	15788.4645	1290.121184	2477.471313	139.684	12772.48964	25220.99029
30719	8302.11	9172.895	3597.42	17440.31	15913.77812	1313.933837	2444.887585	140.211	12843.70683	25292.64473
31422	8450.21	9312.684	3651.16	17714.31	15817.79979	1306.311836	2434.138376	138.526	12672.89832	25055.62007
31422	8450.21	9312.684	3651.16	17714.31	15864.30239	1326.765668	2409.719577	138.526	12785.35844	25302.50246
30560	8236.37	9108.632	3574.16	17405.47	15833.48378	1305.729215	2404.88094	138.263	12735.97216	25163.18826
30742	8366.32	9191.526	3645.32	17517.73	15933.8875	1318.963387	2432.131021	137.737	12817.44721	25311.10992
30616	8265.53	9162.211	3600.89	17426.89	15759.98	1325.292282	2411.971996	137.421	12762.28423	25185.27313
30740	8341.9	9204.159	3636.79	17507.16	15825.33331	1310.066407	2394.122264	136.105	12728.93942	25107.12735
31320	8407.63	9305.263	3661.95	17663.79	15819.16616	1309.102208	2382.803051	143.105	12762.30787	25171.10428
30696	8301.53	9137.526	3622.11	17402.74	15796.445	1311.111	2379.444	137.684	12777.5	25201.41211
30581	8342	9253.366	3635.79	17518.21	15809.77249	1304.55521	2380.308942	139.842	12782.03736	25186.05801

30882	8395	9272.105	3674.89	17666.58	15924.73622	1301.82747	2390.50279	143.474	12804.05219	25259.61518
30480	8286.89	9160.526	3626.47	17429.32	15803.90063	1289.353419	2368.57428	139.211	12720.11133	25108.15874
30480	8286.89	9160.526	3626.47	17429.32	15791.58138	1290.246534	2351.706036	139.211	12679.26588	25076.31464
30783	8359.16	9276.264	3671	17619.37	15761.84262	1297.957055	2345.558058	141.947	12658.46026	24994.488
30432	8234.32	9135.001	3602.74	17407	15755.30949	1301.909889	2342.236545	139	12752.12658	25024.932
30552	8345.11	9231.527	3658.37	17497.05	15770.96594	1300.197815	2327.33788	142.211	12823.1862	25092.99003
30602	8284.21	9242.947	3627.89	17528.32	15717.63127	1300.154972	2313.185078	143.842	12715.65489	24990.85188
30762	8340.47	9247.315	3645.95	17575.79	15751.98299	1299.029324	2311.127142	143.895	12651.08314	24998.2048
30665	8400.1	9293.685	3682.21	17693.53	15774.21016	1294.456918	2303.083598	144.158	12700.89413	25038.00484
30014	8221.47	9093	3604.47	17308.89	15702.73044	1298.708205	2298.800884	144.684	12673.07983	24938.07091
30159	8303.37	9216.474	3642.79	17463.37	15604.54158	1293.506818	2282.047627	147.368	12567.61275	24794.52674
30347	8346.69	9269.474	3666.95	17589.47	15752.333	1299.556	2280.444	151.474	12715.25	25001.30859
30347	8346.69	9269.474	3666.95	17589.47	15720.94098	1294.906228	2277.750584	151.474	12669.45691	24938.75268
30493	8371.47	9266.104	3681.95	17626.16	15685.55852	1282.660259	2265.741067	149.368	12584.6196	24842.81501
29971	8271.21	9165.001	3644.95	17440.21	15740.68762	1281.636262	2249.260185	156.895	12651.08062	24963.19888
30076	8354.42	9233.052	3647.16	17495.95	15542.64252	1286.561594	2245.754247	157	12583.54099	24774.20413
30141	8291.74	9236.211	3658.89	17546.26	15614.64247	1294.004412	2249.497452	159.316	12508.52651	24673.5116
29881	8282.95	9229.157	3676.68	17488.16	15727.59712	1307.153026	2249.791384	161.684	12586.9642	24906.80583
29931	8287.58	9250.264	3657.58	17508.21	15616.61728	1291.366173	2228.018081	166.158	12553.69696	24707.23792
30137	8355.42	9295.578	3677.58	17646.63	15637.02565	1309.594748	2215.761085	181.842	12609.43295	24833.52636
30217	8407.1	9348.684	3717.37	17727.37	15747.90356	1291.587453	2218.17042	208.105	12602.33167	24894.98367
30155	8331.16	9288.736	3693.32	17546.1	15694.12406	1285.933282	2209.937432	237.789	12644.70394	24816.41206
30102	8415.58	9343.368	3710.16	17724.73	15578.07251	1287.061168	2213.633912	277.316	12638.98014	24747.52728
30102	8415.58	9343.368	3710.16	17724.73	15689.74244	1291.921073	2202.185919	277.316	12759.03643	24876.95157
29941	8390.16	9347.947	3728.47	17715.05	15745.03903	1306.566967	2210.506489	293.684	13028.37276	24990.06699
29901	8359.79	9239.264	3690.74	17532.11	15905.36823	1324.253664	2216.049406	294.474	13255.73239	25158.46312
30082	8461.53	9404.842	3740.84	17758.16	15547.99483	1278.085034	2182.494062	298.158	13204.65723	24721.49929
30075	8450.84	9424.421	3729.21	17761.74	15507.556	1272.889	2178.778	286.316	13197.25	24672.24023
30590	8554.16	9495.738	3802.26	17916.37	15912.36418	1319.23629	2223.433103	266.105	13885.99385	25325.48098
30546	8541.53	9437.105	3825.63	17793.21	15798.02472	1314.844049	2199.635716	238.579	14615.45943	25231.34574
31142	8633.84	9455.79	3947.53	17832.32	15648.70239	1290.912751	2192.994873	219.053	16147.87479	25253.43606
31713	8739.84	9671.737	4101.79	18011.42	16029.22355	1330.10884	2203.457213	202.105	21738.55894	26562.92604
31713	8663.58	9648.054	4048.42	17931.05	15854.67848	1317.859184	2187.959804	186.263	29503.17085	28107.32202
31713	8663.58	9648.054	4048.42	17931.05	15820.51519	1286.658307	2184.761281	186.263	31716.75	29100.26942
31713	8705.9	9779.896	3997.74	18179.37	15886.20248	1301.691767	2184.937569	181.053	31716.75	28684.56981
31713	8647	9740.001	3900.05	18187.53	15865.48428	1309.375664	2182.521484	171	28296.50813	27632.16751
31606	8564.42	9546.736	3891.79	17996.79	15882.33035	1301.541966	2166.834662	163.526	23203.46709	26770.47454

31092	8615.68	9621.158	3859.58	18149.26	15813.84199	1289.043804	2170.472398	166.737	18936.84892	25998.08131
30734	8660.58	9632.37	3882.74	18174.16	15782.7053	1286.100115	2155.161502	174.053	15799.74171	25396.57781
29896	8557.84	9584.843	3836.05	18023.53	15986.60545	1304.874418	2163.22121	168.053	14045.48108	25374.66465
30124	8651	9671.421	3879.9	18176.95	15990.9947	1308.37971	2151.227275	176	13246.47299	25233.7686
29699	8652.84	9709.157	3871.32	18181.53	15936.0418	1307.256362	2135.647913	179.789	12911.86363	25109.7192
29544	8586.42	9585.421	3885.16	18041.32	16026.667	1316.444	2153.111	183.474	12884.5	25272.75781
29348	8599.05	9602.105	3873.37	18053.84	15996.02248	1315.247282	2143.103729	195	12826.02501	25167.49037
29568	8666	9684.422	3889.95	18200.9	15940.31315	1309.049238	2132.623748	212.789	12710.03653	25047.44343
29568	8666	9684.422	3889.95	18200.9	15880.25234	1294.198974	2128.058785	212.789	12624.84866	24982.26817
28975	8552.58	9566.21	3860.32	18069.89	15782.26508	1286.225901	2113.391298	236.105	12546.494	24789.5304
29351	8642.74	9616.474	3901.05	18252.16	15748.10247	1296.079668	2107.822889	272.421	12492.10703	24775.00595
29047	8569.42	9599.368	3900.58	18071.79	15844.55994	1301.309033	2096.384729	305.947	12516.50511	24911.02312
29344	8685.89	9754.474	3928.47	18291.11	15879.98703	1310.011265	2104.399227	328.526	12527.20421	24919.95287
28824	8633.68	9591.262	3906.58	18095.16	15836.35596	1295.450124	2129.30335	319.368	12486.63574	24854.6623
28676	8630	9633.896	3910.89	18106.16	15919.64169	1287.988249	2106.152983	330.316	12512.31255	24891.18771
28945	8655.1	9663	3957.95	18152.79	15760.29143	1279.919225	2079.099654	332.053	12435.88848	24730.01183
28656	8658.79	9682.894	3901.95	18106.89	15764.16327	1280.739342	2072.797611	354.895	12399.42004	24797.37808
28751	8714.16	9737.369	3967.9	18254.73	15847.49866	1290.031685	2089.285282	389.105	12403.23112	24786.90244
28939	8772.37	9816.634	4008	18369.69	15897.53136	1308.529582	2078.332758	414.421	12454.52402	24866.17649
28939	8772.37	9816.634	4008	18369.69	15633.64266	1301.380848	2058.396827	414.421	12322.35517	24553.71111
28006	8557.37	9559.263	3918.63	17914.58	15888.09428	1301.556511	2061.848174	417.263	12453.73408	24900.63701
28435	8758.37	9791.052	4014.84	18310.21	15684.5385	1261.116838	2056.510111	418.421	12172.53849	24511.89771
28544	8814.89	9795.264	4026.63	18330.42	15863.70668	1308.20446	2080.485968	383.632	12462.71501	24764.78258
28613	8746	9811.578	4032.05	18264.16	15865.889	1308.778	2080.778	343.684	12466.25	24767.86328
28400	8797.74	9854.474	4048.53	18299.74	15863.40186	1276.955425	2074.661826	291.368	12353.15001	24734.05535
28396	8855.05	9907.21	4081.53	18368.11	15902.26538	1299.924547	2079.655873	247.947	12479.88877	24864.29242
28236	8741.74	9802.633	4039.79	18244.68	15803.40524	1304.409581	2073.002604	211.263	12341.70099	24629.8116
28538	8887.47	9996.212	4125.89	18537.42	15834.82442	1295.032653	2063.782669	189.158	12406.34189	24745.08976
28454	8943.42	9994.843	4151.16	18468.74	15834.6616	1288.213913	2046.700943	173.632	12448.64019	24792.93718
28098	8848.53	9877.001	4151.21	18405.63	15968.621	1291.084954	2055.87321	161.263	12407.22453	24874.21128
27918	8840	9978.58	4135.32	18416.32	15746.75037	1287.33769	2047.688657	159.158	12324.04732	24599.69642
27918	8840	9978.58	4135.32	18416.32	15859.22479	1289.504119	2042.661043	159.158	12366.06877	24808.04371
28140	8965.21	9977.736	4196.74	18520.79	15860.28439	1300.981919	2042.269046	153.579	12409.67254	24896.34146
27955	8928.32	9988.946	4157.16	18510.58	15897.84282	1297.360373	2041.800927	150.789	12463.89349	24922.25821
28022	8953.37	10004.158	4216.11	18476.53	15859.27649	1287.577039	2043.160225	148.632	12436.26913	24807.45306
28442	9105.48	10136	4264.05	18739.26	15875.06724	1297.892694	2026.036991	149.053	12336.23503	24750.16957
28165	9020.26	10047.106	4265	18608	15773.55244	1288.259103	2021.187405	145.789	12267.46147	24575.36846

28139	9025.31	10144.788	4273.95	18631.84	15707.98889	1286.243432	2028.187078	145.421	12268.34669	24526.84941
27695	9010.05	10046.737	4271.53	18570.32	15812.80952	1299.629841	2015.577139	142.105	12352.30918	24690.10645
28126	9055.42	10143.789	4277.26	18647.05	15881.03241	1304.66297	2017.619287	143.789	12331.8467	24732.26073
28048	9114.16	10179.421	4338.63	18707.21	15803.48593	1294.967152	2025.554116	147.263	12267.92136	24623.39699
27669	9037	10138.79	4343.47	18635.95	15728.111	1285	2019.778	147.158	12278.5	24557.92969
27908	9197.84	10230.843	4406.68	18775.74	15777.7845	1292.006441	2013.351261	145.842	12309.91516	24608.03836
27519	9107.21	10211.105	4355.58	18692.79	15826.98704	1301.563646	2008.80247	151	12329.06009	24644.63148
27519	9107.21	10211.105	4355.58	18692.79	15850.98271	1312.641136	2013.869084	151	12357.83062	24661.44505
27938	9220.42	10316.157	4438.16	18870.69	15877.75666	1311.58965	2005.833083	147.053	12370.97659	24657.28405
27635	9182.26	10246.211	4436.26	18765.69	15819.49758	1289.844932	1998.578825	141.632	12269.87467	24544.6401
27594	9209.79	10285.63	4467.9	18758.79	15887.38958	1317.27299	2008.200656	145.368	12373.53345	24689.11186
27478	9227.68	10314.632	4496.79	18794.9	15880.63163	1320.020649	2002.393476	154.263	12348.73618	24672.29661
27533	9287.32	10356.946	4497.95	18865.89	15833.00521	1302.638463	2000.659449	159.421	12328.62538	24608.20014
27622	9397.32	10441.685	4590.1	18974.95	15799.22685	1300.379128	1985.270298	166	12209.02725	24503.2817
27200	9275.21	10343.158	4539.68	18738.16	15865.67123	1319.973582	1998.609858	173	12267.06685	24543.46095
27716	9412.58	10486.053	4601.68	18952.95	15862.76195	1320.310158	1997.153848	207.737	12355.00191	24593.84399
27014	9301.58	10362.842	4588.26	18798.53	15914.36366	1306.264138	2004.494896	250.684	12302.10785	24658.7782
27449	9458.1	10544.212	4684.37	19033	15888.7633	1301.011001	1992.049766	307.842	12253.24503	24507.35697
27182	9409.79	10497.212	4659.53	18961.95	15804.18294	1311.081078	1985.428109	344.421	12202.14627	24415.00377
27128	9454.26	10554.054	4700.63	18962.74	15719.22121	1315.50486	2005.991056	364.684	12252.94645	24435.65596
27128	9454.26	10554.054	4700.63	18962.74	15977.10995	1329.73602	2014.376161	364.684	12434.36205	24674.39884
27232	9472.74	10603.58	4722.74	19016.53	15805.32518	1316.987345	2000.330352	365.579	12306.77187	24473.67595
27010	9569.53	10655.631	4810.9	19090.21	15976.92827	1337.258532	2011.907633	347.053	12387.02805	24686.90425
26719	9407.32	10520.158	4739.37	18900.58	15865.69782	1314.890506	1987.558708	300.789	12248.06869	24552.68208
27107	9611.89	10680.475	4866.16	19119.63	15939.33751	1333.950753	2001.554017	265.316	12412.41331	24534.47889
26734	9553.05	10617.474	4823.9	18985.95	15947.444	1336	2003.111	229	12429.75	24533.61914
26914	9611.32	10741.264	4849.68	19202.79	15939.37896	1327.270557	1976.447856	202.737	12375.73598	24574.49326
26779	9626.79	10652.367	4896.63	19004.58	15783.59375	1323.021823	1967.295923	186.053	12191.69801	24316.1785
26605	9597.26	10685.21	4879.47	18988.84	15810.50607	1329.100676	1954.440602	181.053	12239.25257	24347.64045
26890	9744.79	10792.37	4988.31	19232.05	15877.30098	1343.120677	1971.243968	186.105	12245.27052	24485.45069
26592	9618.21	10728.211	4935	19023.47	15821.62221	1332.816772	1967.776501	185.474	12215.66604	24295.27394
26610	9703.74	10765.896	4991.42	19069.37	15875.1402	1329.829749	1979.66861	196.474	12248.15499	24377.19969
26504	9713.9	10829.157	4999.58	19191.21	15853.89119	1328.261818	1971.369308	223.421	12234.40636	24323.2132
26436	9719.21	10824.843	5029.95	19140.42	15837.34245	1332.506925	1963.127138	264.579	12213.3209	24240.29552
26343	9622.84	10828.578	4989.16	19047.05	15823.28666	1337.401296	1947.321185	343.211	12248.55567	24239.79962
26343	9622.84	10828.578	4989.16	19047.05	15786.03321	1345.324323	1944.315436	343.211	12213.17088	24241.34707
26512	9704.84	10873.264	5047.05	19085.79	15832.50889	1349.859388	1952.557812	443.263	12178.57063	24234.44811

26280	9753.89	10885.896	5057.53	19181.95	15826.8036	1348.656475	1962.668743	539.053	12170.14507	24249.47585
26298	9856.53	10986.211	5144.47	19297.63	15792.42429	1364.21128	1960.271465	613.842	12206.28347	24247.34787
25661	9633.58	10732	5026.16	18869.84	15713.08533	1367.466823	1947.121185	621.211	12184.48405	24100.66106
26408	9937.42	11038.053	5212.16	19370.95	15743.66138	1357.141224	1944.949448	624.579	12150.10558	24094.83179
25917	9858.74	10884.948	5185.63	19158.42	15789.42419	1369.283929	1945.089576	554.895	12162.55656	24181.83095
25738	9803.42	10860.053	5135	19047.63	15707.5948	1380.719506	1940.58158	473.632	12085.75158	24099.18681
26178	10091.89	11185.055	5287.58	19576.05	15759.19012	1374.839895	1939.630078	415.421	12068.8264	24107.85461
25866	9931.1	10971.579	5239.89	19220.43	15786.94466	1371.893995	1932.399478	329.895	12126.60461	24122.27274
25721	9920.05	10975.632	5231.26	19164.26	15850.24106	1387.464442	1934.216699	282.632	12099.92117	24106.7301
25905	10049.84	11131.368	5351.37	19382.63	15807.5711	1397.152912	1948.080141	231.263	12092.83894	24025.8285
25687	10047.1	11101.158	5347.79	19314.21	15684.24256	1381.954669	1940.352464	205.105	11998.36156	23913.68093
25861	10139.47	11194.683	5398.1	19412.79	15854.99379	1398.170801	1934.940166	192.211	12082.28691	24147.68463
25596	10074.58	11113.896	5403.84	19335.58	15770.78373	1400.609726	1922.43177	175.895	12085.39878	24056.78962
25596	10074.58	11113.896	5403.84	19335.58	15630.444	1395.222	1924.778	175.895	12010.5	23868.75586
25742	10091.37	11185.052	5445.68	19389.53	15684.47762	1397.534338	1927.469657	167.105	12034.25002	23924.72604
25982	10332.21	11446.948	5584.95	19721.26	15955.37274	1408.65134	1941.916456	160.526	12162.29849	24212.89915
25698	10164.05	11301.474	5514.58	19493.37	15900.50181	1403.675255	1944.474343	151.474	12186.65596	24191.46248
25851	10354.21	11451.579	5610.89	19672.58	15840.58448	1403.612917	1936.690552	157.474	12091.46318	24035.97956
25747	10326.47	11370.737	5624.05	19577.53	15840.56282	1390.967063	1960.022845	149.316	12085.12089	23984.74469
25860	10351.84	11440.159	5643.95	19646.79	15723.95001	1383.149039	1936.774804	150.158	12088.6198	23959.28017
25699	10304.26	11458.527	5671.53	19573.37	16022.13242	1419.97643	1967.554528	144.211	12324.8439	24371.65846
25561	10326.47	11380.211	5653.42	19456.16	15739.35754	1382.86553	1933.973239	142.737	12041.17042	23939.96404
25717	10402.42	11517.473	5732.53	19710.16	15649.90959	1369.221824	1931.006647	145.684	11979.78021	23772.73127
25794	10537.42	11613	5798.74	19799.9	15961.39179	1398.18636	1932.513337	140.316	12191.15077	24255.46228
25781	10509.37	11588.421	5787.79	19690.16	15816.4852	1381.812649	1911.11787	142.053	12044.13612	23972.44906
25689	10602.58	11723.684	5842.21	19888.37	15812.77096	1377.425922	1904.136914	137.737	12069.47733	23925.00504
25512	10529.89	11616.895	5808.74	19728.89	15925.91055	1372.680864	1931.042427	139.263	12065.62239	24107.35816
25528	10566.63	11676.896	5880.53	19844	15730.18209	1344.219467	1911.159324	138.789	11866.7991	23739.38197
25589	10555	11671.579	5861.1	19854.05	15834.90185	1360.619114	1919.879135	142.158	12048.33784	23932.87505
25589	10555	11671.579	5861.1	19854.05	15852.04336	1363.845469	1914.92092	142.158	12049.4257	23937.31763
25401	10668.74	11774.526	5930.37	19984.9	15807.28843	1354.505446	1926.89999	145.21	12052.80275	23935.31268
25288	10535	11672.58	5847.16	19776.48	15806.35654	1359.562403	1932.701167	141.895	12047.52795	23933.18623
25554	10668.05	11826.579	5927.68	20042.79	15886.726	1349.709462	1946.696567	154.158	12092.07658	23999.64159
25140	10460.53	11650.791	5826.32	19712.27	15898.0527	1357.676638	1930.003921	159.316	12049.25396	23940.01733
25390	10622.16	11782.844	5921.26	19980.32	15769.73535	1345.326713	1910.486743	162.684	11996.75321	23832.39139
25019	10510.32	11730.527	5860.37	19945.37	15760.83852	1329.802379	1927.090684	164.421	12008.89531	23834.40618
25573	10610.47	11809.211	5903.79	20063.16	15758.53961	1321.821816	1929.161524	161.684	11994.4053	23773.48338

25097	10427.16	11669.054	5751.05	19829.16	15780.49348	1327.487983	1935.436522	156.947	11984.43078	23773.24425
25075	10483.05	11689.632	5804.37	19868.63	15778.73405	1330.188775	1922.310398	156.632	11979.30951	23759.55297
25076	10432.84	11662.104	5773.89	19873.58	15669.51177	1317.406925	1904.37451	154.842	11906.66523	23627.75751
25166	10427.74	11713.421	5759.37	20068.63	15655.71	1308.291771	1915.580788	149.211	11867.33921	23613.90121
24693	10271	11473.368	5659.89	19742.95	15702.14795	1303.18068	1902.450995	141.737	11871.447	23630.36881
24756	10328.53	11666.685	5660.74	20001.89	15596.26036	1296.98724	1874.683968	146.947	11815.35334	23466.32707
24683	10284.26	11578.527	5663.1	19903.37	15497.88805	1297.125099	1875.777837	148.737	11796.59272	23354.78421
24676	10268.58	11578.738	5590.74	19968	15592.21956	1306.929391	1910.094496	154.263	11843.43499	23503.87689
24606	10159.73	11471.053	5522.47	19826.42	15617.667	1304.778	1920.778	163.632	11881	23622.0332
24574	10123.74	11464.422	5470.95	19911.68	15535.76417	1293.804098	1910.358952	184.158	11792.29657	23459.72931
24574	10123.74	11464.422	5470.95	19911.68	15416.83098	1276.833441	1887.074107	184.158	11653.68243	23173.33051
24190	9977.89	11274.737	5359.05	19640	15614.21043	1305.787475	1888.880035	196.316	11864.59452	23467.08122
24423	9938	11339.737	5370.16	19704.05	15341.74068	1282.340134	1858.78421	204.158	11629.3788	23088.90114
24411	9997.47	11328.632	5363.11	19758.26	15489.60477	1278.478862	1876.851295	195.053	11656.69377	23250.44528
24148	9865.74	11293.104	5279.42	19717.15	15560.95166	1304.823468	1878.240199	187.895	11724.32024	23284.47698
23925	9805.47	11158.527	5219	19541.89	15471.25446	1274.964234	1868.21841	171.158	11773.06286	23178.67779
23958	9816.32	11174.895	5201.05	19645.52	15440.02059	1280.852449	1850.665693	159.421	11589.33022	23130.78021
23913	9745.32	11140.998	5148	19534.53	15381.20854	1270.66078	1880.831398	153.474	11608.14922	23036.36213
23960	9793.53	11191.053	5188.1	19686.26	15300.69062	1271.121089	1853.761702	147.368	11589.3267	22901.71288
23675	9645.68	11000.264	5083.32	19483.47	15563.47145	1290.427726	1856.987542	148.368	11729.61442	23166.02652
23621	9747.84	11152.476	5107.68	19670.27	15081.62958	1250.328631	1826.291141	149.474	11327.72453	22526.71874
23643	9767.37	11114.578	5121.42	19630.89	15348.62167	1267.600364	1870.181541	144.579	11649.36006	23019.23629
23603	9669.16	11141.264	5083.68	19670.21	15329.81949	1272.744466	1871.656788	148.842	11578.15039	22974.43178
23467	9623.32	11037.632	5040.74	19486.52	15411.49944	1287.644984	1851.979214	150.158	11650.72939	22974.71637
23347	9657.74	11088.63	5072.37	19632.53	15336.05983	1270.953416	1835.567344	157.368	11681.87121	22881.08406
23674	9711.37	11144.211	5063.05	19730.21	15275.523	1263.736127	1846.032851	159.053	11702.55977	22825.12003
23746	9719	11190.684	5060.21	19814.42	15460.96625	1289.607865	1851.155987	164.526	11882.87255	23097.15468
23736	9706	11162.265	5065.47	19808	15311.83927	1264.304134	1831.513596	179.632	11993.04272	22909.30738
23522	9665.89	11131.156	5033.74	19766.63	15327.74181	1259.173309	1834.293403	194.368	12021.07827	22870.28297
23574	9680.53	11159.79	5046.16	19846	15445.21744	1278.786896	1853.039938	217.053	12062.00226	23081.90839
23574	9680.53	11159.79	5046.16	19846	15400.55701	1264.19789	1849.519685	217.053	11828.90929	22923.52051
23834	9757.79	11299.735	5069.58	20089.05	15389.88166	1272.307624	1848.378724	228.789	11777.57068	22895.14201
23625	9665.9	11184.053	5028.74	19935.1	15517.40536	1289.471893	1866.61942	234	11691.40393	23000.99513
24070	9814.53	11332.947	5095	20179.05	15499.79845	1280.866431	1855.421459	240.263	11632.15484	22961.39571
23925	9713.11	11273.736	5021.1	20055.73	15467.33954	1273.484969	1830.409628	231.421	11585.65259	22896.58991
23791	9742.42	11320.421	5042.37	20168.95	15423.20173	1278.190017	1837.079177	228.053	11553.56752	22873.15118
23829	9791.63	11313.368	5035.68	20158	15472.56712	1283.042436	1857.83321	221	11640.9711	22939.03148

23729	9666.47	11245.475	5003.11	20077.37	15554.2646	1290.195797	1870.469589	222.421	11653.32985	23002.27354
23759	9752.42	11284.105	5024.58	20158.47	15555.09845	1290.446	1868.100448	240.105	11598.95402	23000.24396
23719	9767.21	11355.263	5034.42	20284.1	15452.52427	1274.371519	1847.492403	275.895	11540.1439	22893.63074
23514	9625.68	11243	4954.53	20134.58	15454.68536	1276.699028	1851.799372	323.053	11538.19623	22933.72431
23731	9713.53	11354.106	5008.95	20284.63	15549.90425	1288.842732	1868.404122	386.789	11588.39684	23029.32781
23411	9575.26	11230.685	4971.58	20054	15513.81862	1280.159249	1861.683326	443.737	11549.10004	22940.67638
23379	9556.47	11241	4952.32	20132.74	15582.48117	1282.879927	1860.270469	493.526	11533.23389	23002.44115
23298	9570.89	11265.685	4930.21	20205.74	15382.02845	1277.172564	1824.591085	558.316	11362.19021	22722.72828
23094	9550	11219.474	4933	20125.79	15408.54486	1287.718909	1831.327099	604.789	11479.49963	22861.15067
23065	9601.26	11282.736	4902.26	20197.69	15424.68606	1286.682601	1837.36549	629.421	11439.84845	22846.64391
23302	9577.58	11243.158	4907	20165	15541.45382	1273.95073	1834.157388	641.053	11444.44135	22928.3526
23028	9617.48	11196.104	4923.37	20104.95	15388.22243	1261.754447	1806.79505	584.316	11344.73189	22654.77338
22770	9492.79	11120.789	4872.95	20009.9	15457.64915	1274.985906	1838.421183	486.842	11388.62444	22776.53523
22866	9620.95	11224.946	4923.58	20181.32	15436.99929	1287.111429	1844.872714	411.526	11442.40169	22774.00833
22832	9573.58	11189.369	4913.26	20110.9	15231.05722	1261.186376	1837.668198	329.579	11283.99019	22474.35133
22692	9555.16	11186.474	4927.79	20106.26	15352.12816	1273.715913	1804.884094	256.474	11320.87753	22633.60806
22692	9555.16	11186.474	4927.79	20106.26	15419.91085	1289.434208	1816.885138	256.474	11336.21844	22701.66718
22891	9545.74	11239.107	4892.63	20152.26	15172.78399	1255.105859	1787.86586	206.526	11189.22684	22268.57264
22591	9605.16	11252.369	4934.58	20202.21	15321.53634	1274.864271	1807.078902	176.105	11278.24677	22549.82076
22782	9603.05	11258.896	4923.53	20220.1	15135.16401	1269.786525	1800.48814	160.684	11222.0843	22387.47991
22506	9467.68	11071.894	4841.32	19918.37	15114.11663	1253.215433	1819.842542	141.579	11159.77605	22249.02475
22655	9646.68	11268.842	4979.95	20278.84	15161.56755	1256.737512	1787.396084	140.895	11222.15839	22393.90697
22852	9614.42	11223.315	4962.1	20197.26	15043.70739	1248.271779	1797.069812	137.316	11063.99104	22146.97008
22508	9485.16	11125.315	4912.95	20071.84	15176.76875	1260.600759	1786.621229	133.368	11127.21706	22294.19277
22604	9665.58	11347.736	4949.26	20320.63	15205.98502	1263.784762	1795.398839	136	11174.99747	22365.45672
22608	9657.37	11313.789	4967.26	20259.95	15117.74535	1253.00648	1778.161547	133.263	11126.21204	22148.02452
22485	9600.21	11262.632	4938.1	20174.21	15090.44754	1248.877307	1785.417197	128.105	11118.34134	22101.95273
22311	9561.21	11205	4950.95	20099.05	14906.47708	1234.255615	1766.165977	126.053	11003.79623	21920.77934
22092	9570.68	11194.265	4905.84	20100.84	14953.77674	1240.750106	1767.787812	125.579	10984.99367	21945.10117
22548	9712.05	11402.737	5034.9	20399.58	14999.667	1251.578254	1771.188709	125.579	10956.99874	22002.38824
21939	9562	11217.315	4939.47	20111.47	15029.61516	1248.389519	1785.648482	125.368	11004.88207	21995.90265
22074	9489.89	11123.21	4899.74	19964.42	14922.23316	1246.017254	1772.605684	119	10935.09559	21883.54564
22410	9700.26	11385.999	5050.74	20305.16	14904.94795	1240.22945	1776.711493	122.895	10955.81515	21923.09133
22094	9606.84	11290.106	5009.95	20101.89	14922.08362	1229.043836	1768.42841	119.526	10937.73756	21829.62676
22153	9653.47	11313.842	5025.9	20166.58	14877.12418	1227.385499	1739.564727	120.684	10816.54915	21691.25126
22201	9767.11	11406.368	5110.79	20415.16	14918.28918	1233.25893	1752.978326	123.895	10882.25852	21812.82263
22124	9596.32	11268.895	4972.05	20083.37	14927.21166	1240.166159	1760.912716	120.526	10948.96769	21845.1763

22074	9748.37	11414.104	5118.42	20323.05	14905.6041	1242.465197	1753.519267	119.632	10907.88027	21737.69027
21829	9741.63	11411.684	5116.16	20272.1	14993.93164	1246.973038	1774.318888	118.684	10945.63731	21820.36476
21895	9759.21	11447.106	5126.89	20312	15064.111	1254.778	1790.111	120.053	10991.75	21940.75977
21995	9803.68	11496.525	5177.16	20320.11	15041.41723	1253.766292	1781.930652	120.105	10964.05343	21910.15598
22170	9899	11582.315	5231.47	20520.31	14969.7793	1247.433607	1760.194666	116.474	10907.66728	21818.40695
22009	9917.42	11522.685	5288.79	20423.69	14950.64402	1248.266131	1755.685503	118.842	10914.8068	21794.54107
21871	9868.26	11537.315	5265.53	20358.68	15031.40216	1267.34272	1774.433037	118.684	10955.7935	21866.01005
21869	9959.53	11646.736	5315.11	20467.32	14977.92598	1264.222137	1770.341856	115.263	10906.94411	21761.71289
21794	9955.16	11599.737	5335.95	20363.16	14888.44922	1253.81941	1770.558856	116.421	10877.94049	21674.55276
21794	9955.16	11599.737	5335.95	20363.16	14947.61742	1269.049209	1752.690762	116.421	10856.91895	21698.13837
21890	10056.58	11756.684	5395.79	20581.84	14967.28036	1255.30978	1763.129098	114.526	10919.87679	21768.58441
21738	10048.89	11645.578	5455.05	20455	14941.01709	1233.954333	1762.648352	116.421	10897.48633	21710.14245
21633	10060.42	11680.79	5446.37	20416.89	15095.79436	1253.797508	1769.197526	117.105	11009.93263	21906.8495
21649	10170.47	11750.896	5503.63	20549.84	15045.73881	1253.628659	1775.533488	112.053	10963.83433	21851.95236
21746	10162.26	11788.526	5544.58	20572.58	15104.94245	1246.676283	1784.957498	115.895	10965.27494	21870.40182
21310	10082.42	11732.263	5529.58	20423.26	15109.04698	1246.540675	1782.055989	117.053	10922.38208	21853.84395
21852	10185.74	11859.157	5609.37	20602.1	15112.88823	1259.261148	1777.844334	115	10985.60503	21884.14261
21801	10289.26	11989.525	5686.9	20725.68	15109.06324	1257.455511	1773.576317	116	11055.05258	22010.93424
21321	10069.74	11769.053	5545.95	20400.9	15016.57865	1271.176704	1763.419853	114.526	11003.50954	21796.58119
21692	10312.16	12029.526	5705.9	20808.53	15102.49117	1251.529069	1784.197128	117.053	11007.74187	21864.32082
21362	10110.79	11736.211	5560.79	20386.16	15038.06253	1258.270766	1763.311804	117.053	10939.04443	21782.23104
21379	10177.58	11851.578	5619.63	20553.79	15042.03128	1258.789345	1758.463113	114.632	10872.00798	21786.64227
21499	10193.37	11905.999	5593.89	20649.84	15063.23008	1268.450229	1791.383606	114.105	10940.92531	21810.01621
21186	10158.79	11865.473	5566.05	20662.58	15018.29082	1241.710202	1762.53782	118.263	10898.13096	21696.66243
21448	10085.63	11840.158	5526.84	20659.74	15023.00568	1244.955809	1769.532856	116.737	10941.57508	21749.59638
21378	10023.95	11807.79	5462.11	20596.79	14882.48947	1230.532375	1754.712337	112.053	10818.78881	21551.23528
21037	9924.9	11684.263	5401.63	20459.9	14924.10754	1238.434343	1748.369663	114.474	10816.99511	21566.54696
21318	10029.42	11855.579	5429.47	20783.37	14954.11005	1240.38137	1745.774124	117.316	10880.88457	21633.62972
20689	9696.95	11485.315	5207.26	20244.53	14933.2393	1242.640568	1760.807381	111.895	10885.81632	21547.53686
21123	9849.47	11736.895	5268.05	20680.21	14943.02913	1234.263613	1744.734124	112.737	10824.77687	21530.44663
21103	9785.79	11650.209	5197.58	20602.53	14977.3086	1245.813753	1734.393748	109.421	10779.84965	21489.91187
21017	9716.63	11568.264	5135.79	20571.37	14915.76887	1242.12767	1744.401814	114.789	10811.21632	21459.84004
20811	9602.95	11500.735	5013.21	20511.58	14970.37152	1242.073626	1756.730045	117.105	10811.57997	21542.25641
20697	9515.37	11423.736	4954.74	20480.32	14938.69491	1243.952208	1746.649331	109.105	10808.78757	21524.84903
20944	9597.68	11537.473	4963.53	20726	14870.9943	1238.634057	1735.794915	107.947	10793.65894	21425.80408
20528	9402.05	11307.842	4798	20406.42	14801.66435	1234.917276	1732.766021	115.947	10694.42423	21317.65641
20560	9379.16	11273.526	4766.16	20462.58	14816.91669	1243.971496	1742.333033	111.316	10689.2125	21371.33934

20910	9395.05	11354.735	4781.89	20621.21	14865.97489	1253.280287	1747.290888	113.842	10738.49367	21421.29098
20559	9243.79	11234.895	4680.47	20404	14793.30165	1244.330002	1733.102477	116.211	10680.35205	21281.47226
20469	9253.32	11174.947	4644.95	20412.79	14777.2437	1236.621902	1728.155747	111.947	10654.99028	21204.48074
20438	9259.68	11239.368	4637.47	20559.1	14793.77588	1233.383699	1728.472925	114.421	10671.25404	21199.00578
20360	9198	11196.579	4577.79	20488.74	14806.99026	1227.058667	1726.38098	113.316	10707.84309	21245.78655
20233	9132.05	11132.843	4540.74	20392.79	14793.34115	1234.956485	1722.561117	112.632	10783.40267	21236.40268
20194	9119.68	11038.315	4493.95	20369.42	14729.9684	1231.596612	1720.404753	117.211	10729.87349	21143.44346
20253	9126.84	11127.317	4496.32	20447.63	14677.39948	1216.047981	1715.928642	114.947	10670.36841	21048.27738
20243	9117.05	11125.526	4493.74	20505.42	14696.63257	1230.161206	1713.597587	112.789	10717.81187	21151.35514
20091	9077.21	11117.422	4434.84	20455.68	14660.36142	1230.837673	1702.317642	115.421	10659.20793	21074.57602
19800	9017.42	10974.736	4384.63	20274.63	14654.0367	1228.830919	1700.356591	113.579	10638.42793	21091.17019
20031	9121.53	11170.527	4447.21	20560.53	14599.61126	1230.876715	1711.261479	116.579	10609.021	21023.92037
19823	8957.84	10947.789	4355.42	20258.11	14566.55556	1203.468021	1700.359231	111.947	10515.51656	20892.18371
20054	9101.32	11154.211	4422.74	20627.42	14683.07011	1222.057197	1700.55839	115.105	10588.41217	20994.72147
19520	8854.53	10888.737	4321.47	20140.95	14549.66604	1218.577946	1695.628846	111.789	10480.48746	20800.66369
19723	8974	10991.368	4347.84	20377.47	14684.59771	1234.736723	1727.539928	111.895	10631.15207	21019.54614
19487	8948.79	10960.789	4331.37	20286.47	14594.53446	1212.752433	1700.707688	108.105	10462.02799	20896.03287
19804	9037.84	11119.738	4356	20537.21	14721.1582	1227.877736	1703.840683	114.316	10561.46717	21086.57841
19439	8919.16	10935.314	4306.1	20288	14545.57477	1220.771857	1707.930986	111.053	10477.33734	20842.70832
19439	8919.16	10935.314	4306.1	20288	14580.023	1226.436343	1697.780489	111.053	10465.13329	20791.0716
19767	8935.63	11027.423	4315.42	20376.26	14479.92369	1217.571358	1694.796156	113.368	10430.68435	20696.64315
19576	8992.16	11021.577	4319.05	20460.32	14513.45844	1220.247958	1685.034036	111.737	10469.40166	20746.58999
19434	8834.89	10911.473	4261.42	20224.84	14480.95056	1214.569859	1674.355635	111.632	10371.18409	20674.36289
19214	8888.05	10970.947	4300.79	20306.37	14619.79517	1223.547849	1696.149807	109.632	10490.64189	20879.71733
19465	8989.79	11031.578	4332.63	20478.37	14492.34614	1225.865828	1679.881715	112.368	10402.59962	20663.20497
19200	8801.68	10879.579	4250.32	20186.37	14445.47102	1226.228045	1674.816092	110.684	10393.58275	20596.48398
19251	8911.89	10996.105	4287.79	20419.68	14474.18826	1222.242959	1676.881934	110.842	10433.80505	20658.14944
19168	8871.05	10884.789	4239.47	20250.31	14433.76204	1203.383359	1691.014958	111	10357.05561	20524.64062
19116	8831.32	10902.369	4234.95	20222.95	14420.15516	1209.459026	1676.0575	110.211	10314.37416	20513.7709
19256	8921.26	10977.317	4291.79	20430.79	14397.6196	1211.676635	1667.387557	110.105	10281.7992	20529.03575
18931	8795.11	10921.369	4236	20241.84	14445.77152	1214.976525	1683.804051	109.368	10295.70057	20601.51804
19128	8881.79	11011.158	4269.63	20387.53	14462.77483	1214.769793	1691.740133	107.632	10293.7861	20596.94657
18877	8914.21	10955.21	4281.42	20383	14448.90604	1211.810647	1674.768178	111.053	10275.37089	20543.21913
18792	8824.53	10973.473	4250	20302.26	14380.76733	1212.116516	1656.150917	106.737	10215.26576	20429.42907
18818	8849.53	10953.369	4240.79	20301.68	14319.72758	1214.950647	1652.728647	106.789	10192.06141	20348.72636
18815	8779.95	10897.685	4222.05	20147.31	14343.0709	1202.276767	1662.464558	104.842	10196.85786	20357.08016
18777	8849.95	10945.263	4232.1	20363.58	14341.88389	1199.231514	1673.975422	104.737	10156.97332	20335.55658

18709	8880.16	11010.789	4284.21	20426.52	14325.54728	1214.656613	1672.579217	108.316	10148.36363	20341.1909
18628	8868.26	11019.21	4260.84	20360.37	14283.02863	1200.813508	1665.847869	105.789	10151.18089	20326.74626
18449	8776.9	10908.423	4208.42	20234.21	14255.8217	1186.627544	1673.764651	106.263	10167.86735	20283.24507
18527	8860.68	10980.525	4246.74	20372.32	14329.41246	1204.554876	1673.305727	102.053	10218.23599	20305.51003
18462	8755.74	10898.685	4194.74	20212.31	14310.43117	1211.329211	1654.806211	104.158	10244.10856	20258.90794
18317	8753.42	10840.842	4188.68	20153.47	14398.6139	1207.529326	1662.316597	105.474	10428.3942	20388.98874
18426	8839.05	10993.842	4246.47	20341.89	14269.49782	1213.412062	1652.47524	102.789	10540.4789	20281.8913
18064	8726.05	10839.473	4206.37	20105.21	14210.06145	1207.687234	1645.608659	106.053	10544.86255	20102.80933
18223	8758.63	10875.105	4202.79	20188	14216.07246	1191.406916	1648.136745	107.684	10532.24643	20152.72658
18361	8847.47	10966.841	4223.16	20342.84	14312.70338	1216.832423	1656.721086	102.526	10504.6974	20269.60177
18054	8760.05	10874.843	4213.74	20198.21	13976.0852	1175.523473	1629.595914	107.526	10133.84277	19806.92627
17948	8702.32	10794.633	4212.32	20037.63	14354.13136	1209.344179	1648.606435	109.316	10351.90482	20267.75045
18101	8773.63	10887.053	4206.84	20190.63	14142.34524	1193.200854	1634.023805	109.053	10111.25035	19975.73971
17942	8725.16	10885.685	4196.95	20113	14277.25139	1190.374088	1649.362103	103.263	10175.42855	20165.67182
17660	8685.68	10804	4185.68	20011.63	14042.16282	1183.521464	1637.70911	104.895	10012.68676	19893.63565
17649	8674.42	10803.475	4171.47	20039.05	14255.90903	1208.833272	1654.73655	105.053	10069.04645	20139.60653
17815	8742.68	10903.685	4205.37	20206.53	14042.09865	1186.037152	1613.249634	109.789	9954.3368	19841.03032
17563	8668.21	10856.631	4191.58	20064.53	14101.83214	1205.859138	1632.217934	106.579	9887.879952	19891.80873
17797	8721	10916.264	4178.26	20190.05	14132.75861	1207.600702	1636.423884	107.895	9945.006278	19958.39191
17403	8714.05	10847.421	4183.42	20069.21	14002.69626	1180.787503	1637.673611	104.789	9824.022115	19744.35564
17627	8701.42	10888.105	4181.05	20138.47	14132.28523	1199.668801	1612.107845	104.053	9974.806273	19922.17628
17531	8664.16	10857.737	4170.79	20057.47	13915.87912	1188.115222	1619.894838	106.684	9812.318115	19635.92011
17480	8704.84	10847.526	4201.58	20133.63	14025.4243	1184.183835	1629.93761	105.737	9856.078036	19776.80724
17538	8746.16	10888.842	4205.53	20164.16	14001.87216	1188.483582	1632.815248	103.947	9886.81107	19744.94962
17369	8628.95	10771.579	4155.26	20023.69	13962.88204	1184.037706	1611.874885	104.368	9830.821451	19637.38092
17436	8678.21	10876.156	4192.26	20164.95	13912.94496	1180.936193	1597.799293	103.789	9752.095797	19559.7793
17352	8650.26	10842.895	4179.16	20075.42	13869.11145	1186.301634	1599.780921	102	9786.657365	19555.94344
17228	8670.05	10840.738	4171.79	20071.11	14027.08494	1205.410127	1611.33245	103.789	9801.547057	19708.09943
17248	8664.26	10869.736	4167.21	20065.1	14085.47233	1195.589076	1615.412672	105.368	9829.691647	19775.2352
17057	8629.21	10832.894	4146.74	19990.89	13906.32232	1178.750989	1600.814757	101.368	9747.91687	19586.05191
17248	8660	10862.422	4150.53	20045	13896.26792	1184.116268	1603.162846	103.684	9704.585106	19538.87081
17076	8681.53	10890.159	4195.53	20186.37	13921.94972	1196.153395	1600.763533	105.263	9754.140081	19577.18184
17056	8556.79	10732.737	4119.26	19868.37	13817.00558	1185.111604	1581.105043	101.211	9675.763937	19385.67206
16947	8583.37	10793.685	4131.63	19958.37	13862.43695	1179.414945	1592.742511	100.053	9677.91901	19403.63365
17108	8607.37	10803.105	4165.05	20031.16	13887.23983	1180.159381	1610.330952	108.368	9721.908557	19485.29806
16957	8611.05	10862.053	4155.32	20015.58	13898.80889	1178.657434	1608.259598	104.053	9711.424696	19472.01321
16943	8616	10791.157	4128.31	19979.58	13901.65088	1179.841137	1609.91442	104.842	9690.831343	19436.4011

16927	8607.32	10810.736	4152.79	19992.31	13795.69478	1178.878918	1608.535752	100.947	9629.366421	19325.71509
16842	8616.32	10795.264	4132.79	19943.05	13897.07541	1191.007183	1605.063574	101.632	9709.499621	19458.30274
16818	8681.16	10915.158	4173.63	20127.27	13896.20307	1193.655597	1590.890707	102.842	9700.365932	19445.97342
16745	8621.79	10812.736	4145.21	20020.84	13757.47113	1176.556887	1568.131864	102.632	9555.020639	19230.02883
16665	8579.47	10775.105	4142.84	19949.37	13803.75528	1173.898904	1580.909427	102.263	9632.999469	19260.08804
16622	8570.58	10796.317	4110.9	19951.37	13817.12957	1184.070835	1603.273347	101.263	9629.566379	19308.81187
16776	8651.53	10875.684	4160.05	20071.11	13910.93158	1184.880588	1603.371555	102.684	9748.748381	19492.07673
16750	8607.37	10866.053	4145.47	20088.69	13660.56062	1174.620128	1586.915258	101.105	9587.250431	19155.86832
16480	8573.89	10752.474	4140	19905.63	13684.61097	1180.551661	1601.463773	104.211	9577.875259	19181.38797
16509	8565.63	10774.475	4121.26	19880.58	13648.50946	1175.75223	1583.026318	104.316	9573.787436	19166.99292
16404	8583	10836.63	4159.16	19952.58	13844.51251	1177.182852	1597.735585	102.421	9618.708959	19331.44308
16745	8615.58	10871.475	4150.79	20043.58	13753.34147	1169.183446	1568.910386	102.263	9478.683908	19154.10679
16599	8535.89	10809.842	4127.58	19961.31	13815.62229	1176.61606	1593.806736	101.632	9563.157444	19238.96879
16098	8512.79	10766.527	4122.53	19814.9	13569.56357	1155.466189	1580.79936	102.579	9475.031819	18980.34945
16313	8594.63	10834.421	4132.26	19976.11	13797.91128	1175.255654	1608.490522	101.053	9673.51695	19320.76613
16365	8543.58	10789.896	4119.68	19879.68	13483.9614	1156.139702	1548.659257	101.632	9438.507994	18862.52942
16362	8560.42	10796.158	4114.68	19913.9	13673.32761	1168.441395	1582.543222	98.842	9495.388232	19072.12326
16222	8556.16	10790.63	4120.68	19877.21	13757.34779	1186.815465	1575.544077	100.105	9552.123862	19090.75669
16139	8455.26	10707.104	4067.37	19774.11	13556.67764	1159.486228	1556.799526	98.158	9404.257585	18934.54521
16171	8556.47	10794.105	4120.95	19894.05	13604.76748	1154.117748	1580.098968	100.579	9396.088404	18947.44774
15958	8457.21	10679.789	4065.84	19657.37	13532.59494	1153.872874	1565.875277	103.053	9451.473758	18873.15951
16095	8519.11	10803.316	4124.53	19913.26	13624.83675	1154.991592	1576.675122	104.053	9422.91472	18902.01124
16182	8545.74	10844.315	4130.84	19909.16	13610.41814	1170.05069	1565.970759	101.895	9422.591605	18950.83701
15916	8421.53	10695.368	4072.05	19699.37	13515.46619	1169.147128	1556.380732	101.316	9350.038031	18829.61251
15826	8444.26	10668.21	4075.68	19685.47	13432.33608	1163.314701	1542.405156	100.947	9321.30632	18727.61526
15732	8421.74	10665.685	4049.63	19681.21	13400.02908	1157.241216	1565.201323	99.053	9352.305746	18679.35943
15771	8446.58	10668.79	4061.47	19633.32	13526.23263	1164.246846	1566.24431	97.947	9377.553351	18790.1549
15662	8379.05	10613.263	4043.42	19524.89	13416.152	1156.103699	1558.730693	98	9326.990541	18680.24861
15904	8496.79	10774.526	4086.58	19826.9	13376.64407	1146.227851	1544.297613	103.368	9264.522041	18549.48794
15621	8378.11	10656.159	4044	19588.37	13408.64398	1151.649704	1530.292861	96.368	9261.348623	18570.76879
15524	8372.58	10578.738	4059	19560.69	13405.43641	1147.434149	1530.303654	97.684	9302.923796	18649.98346
15589	8372	10638.525	4058.95	19636.79	13366.03505	1152.885383	1540.537275	99.632	9260.172002	18598.36569
15269	8326.9	10611.158	4022.84	19469.58	13292.70313	1158.53685	1535.004093	99.737	9190.809454	18459.30124
15543	8336.84	10603.368	4044.58	19523.47	13286.41788	1148.398485	1525.986323	103.105	9220.035949	18445.24419
15515	8342.68	10609.422	4001.79	19507.79	13326.65977	1145.583785	1530.864901	98.632	9217.205602	18478.75928
15230	8394.1	10656.895	4061.32	19597.84	13250.08657	1147.271114	1527.066399	102.632	9159.591727	18387.2414
15471	8353.79	10658.632	4032.84	19565.63	13207.08072	1142.619744	1518.758987	97.947	9163.487856	18319.59265

15499	8372.58	10628.158	4064.84	19511.63	13287.19851	1144.947291	1521.452842	102	9165.543821	18381.89505
15310	8289.21	10520.841	4011.32	19379.42	13238.89703	1142.264852	1519.978308	97.421	9153.743447	18366.83521
15171	8262.47	10498.737	3981.42	19331.79	13203.65769	1133.802054	1514.614315	98.684	9150.382356	18295.85038
15271	8291.58	10568	4012	19416.21	13230.77546	1151.179645	1507.261962	97.842	9094.440781	18301.09705
15258	8258.58	10563.105	3998.42	19383.84	13164.46009	1144.845374	1502.593404	98.737	9022.967306	18206.55162
15208	8339.74	10620.526	4039.26	19489.11	13186.31835	1143.404569	1512.304456	97.895	9058.921876	18286.77151
15078	8214.63	10476.896	3995.74	19263.47	13144.78332	1142.804412	1507.589618	98.789	9062.499319	18252.37915
15187	8308.53	10603.999	4004.58	19453.79	13110.87482	1136.91782	1505.230727	96.895	9015.011484	18168.9426
15054	8264.68	10499.79	3997.79	19261.26	13242.70069	1151.89471	1494.285776	98.842	9120.136625	18294.86304
15236	8337	10678.209	4038.42	19518.47	13173.83905	1135.923786	1499.18876	98.316	9013.502594	18127.96795
14880	8285.1	10604.684	4017.79	19420.73	13148.49962	1150.309083	1488.009796	99.842	9006.126649	18120.44564
14887	8221.37	10469.789	3972.21	19255.89	13050.29091	1148.294418	1486.170084	95.368	9041.965247	18077.93219
14908	8234.16	10531.316	3981.53	19234.16	12962.08573	1128.260475	1495.515569	97.684	8944.533769	17899.57928
15142	8367.11	10667.474	4031.84	19469.21	13129.72981	1142.662972	1490.510039	99.789	9008.891848	18094.61728
14613	8063.05	10324.104	3905.11	18928.84	13193.01744	1129.486797	1480.034027	94.737	9014.481513	18105.2422
14924	8332.69	10659.105	4028.79	19502.05	12954.70109	1134.400602	1476.229221	99.684	8908.846818	17923.04984
14745	8177.21	10480.052	3977.21	19198.69	12939.27029	1135.392136	1468.055661	97	8870.197092	17874.52405
14798	8277.16	10583.737	4022.37	19396.53	13198.64975	1156.160958	1500.153654	100.158	9042.101992	18127.22572
14581	8176.47	10439.631	3949.89	19125.69	12979.26971	1137.618578	1464.897242	98.158	8949.690527	17895.68035
14874	8308.42	10558.211	4027.68	19355	13047.72268	1148.166775	1488.719078	94	8954.852675	17993.31371
14589	8149.05	10486.895	3975.26	19179.27	12956.62189	1140.637421	1483.286331	95.789	8938.262384	17881.59685
14700	8166.79	10520.737	3947.16	19163.63	12996.63843	1134.470867	1474.794839	96.579	8962.361061	17900.85258
14838	8216.58	10554.79	3991.11	19222.84	12897.81417	1124.133818	1474.083968	96.684	8849.988663	17818.02815
14679	8255.74	10521.105	4005.26	19254.32	12971.08079	1130.750738	1474.831802	97.526	8845.038066	17893.00922
14739	8141.89	10474.474	3951.95	19140.16	12944.76695	1126.60413	1470.036548	95.737	8787.29091	17790.17624
14678	8245.79	10522.843	4007.37	19307.95	12814.39462	1114.312497	1457.029706	99.316	8724.474576	17619.65215
14495	8091.16	10398.105	3911.26	18986.42	12874.94597	1122.745175	1456.839506	98.526	8799.678622	17662.07625
14537	8212.32	10546.053	3977.42	19259.11	12816.72387	1116.571638	1449.658242	95.895	8852.602542	17672.16979
14354	8163.84	10471.052	3970.11	19135.68	12742.41196	1105.312009	1451.335463	97	8739.768991	17511.9727
14322	8121.79	10428.947	3937.53	19054.37	12805.17476	1129.960321	1461.451391	95.737	8768.026697	17560.56161
14307	8076.95	10404.052	3924.63	18976.53	12808.74837	1126.214015	1470.679653	93.368	8775.081874	17614.0763
14506	8176.11	10550.473	3970.47	19205.47	12814.81495	1116.049324	1465.874326	97.579	8764.307538	17612.05134
14291	8178.42	10490.474	3978.32	19157.32	12796.16922	1116.625147	1448.130082	95.526	8712.839487	17530.30211
14261	8041	10393.736	3902.47	18905.74	12672.42143	1113.688278	1433.67579	97.947	8636.38971	17395.24606
14346	8085.89	10436.422	3933.53	18997.31	12684.98878	1128.84344	1434.148613	98.947	8690.053202	17466.79367
14241	8084.58	10406.894	3914.9	19030.58	12777.28121	1131.624879	1439.178711	98.526	8705.679852	17527.97632
13808	7970.26	10260.368	3869.26	18754.42	12741.05515	1113.809873	1432.847145	92.474	8644.004876	17429.76976

14269	8105.05	10427.789	3942.11	19057.74	12679.16108	1104.316212	1418.510942	95.211	8586.691216	17332.18683
14184	8009.84	10310.685	3901.95	18855.32	12628.91692	1104.922871	1410.663201	94.316	8587.625725	17269.77653
14034	8111.11	10455.58	3927.11	19007.69	12671.2208	1120.133204	1425.540796	96.474	8667.479841	17376.20611
13939	8000.79	10290.685	3875.05	18820.47	12656.45	1115.95046	1422.006349	95.053	8601.887967	17302.66517
13955	8011	10368.791	3893.16	18816.21	12621.44783	1108.833522	1427.80609	95.421	8594.387157	17271.7269
14067	8118.11	10462.474	3933	19036	12586.63941	1110.348539	1425.741485	96.842	8534.440772	17169.26066
13791	7941.68	10268.842	3878.26	18691.47	12574.52445	1116.784067	1427.383041	92.947	8530.848209	17199.29876
13952	7979.16	10320.842	3877.53	18778.26	12645.89525	1113.952671	1421.490135	96.158	8595.042022	17323.47202
13803	7961.58	10280.474	3870.58	18710	12575.56359	1090.426188	1398.864455	93.316	8493.546105	17111.50204
14126	8090.47	10507.21	3942.05	19064.58	12604.7294	1103.540879	1418.753569	98.579	8573.157582	17254.0816
13696	7923	10270.159	3864.16	18643.84	12513.04726	1098.973344	1419.333254	95.211	8506.768404	17065.84642
13704	7949.84	10259.894	3848.42	18645	12551.22531	1090.636543	1409.509954	90.737	8527.175957	17125.91432
13610	7922.74	10239.105	3864.68	18645.89	12590.87692	1117.411045	1426.580789	93.474	8501.45379	17132.55475
13867	8001.21	10355.579	3904.53	18841.42	12485.4719	1097.557228	1401.213841	96.211	8525.154668	17071.8811
13699	7923.21	10322.58	3871.05	18739.26	12380.62787	1099.069869	1391.162317	90.105	8415.017873	16934.52162
13692	7916.47	10278.844	3825.89	18615.79	12469.60034	1104.364424	1387.106837	91.579	8415.309137	16925.02037
13825	7988.16	10346.159	3916.68	18802	12429.17892	1105.585279	1375.257163	96.263	8393.239031	16920.28961
13427	7891.05	10250.631	3850.26	18577.58	12491.41728	1106.953152	1375.509042	95.053	8404.607326	16961.96511
13695	8010.05	10422.579	3879.68	18893.21	12403.22435	1097.525899	1381.80143	94.368	8384.684899	16927.28198
13424	7848.47	10173.421	3822.05	18487.47	12488.87558	1100.269592	1406.632078	94.526	8460.585867	17024.97384
13336	7928.42	10286.105	3869.05	18668.16	12344.33318	1094.382777	1372.936185	92.105	8426.807161	16784.42401
13576	7933.63	10387.789	3878	18753.9	12406.65744	1109.586477	1385.092131	94.263	8453.207278	16877.53343
13672	7912.84	10284.79	3856.68	18616.79	12325.36343	1097.955114	1380.832423	92.895	8330.54556	16778.18052
13432	7881.53	10207.632	3849.68	18551.42	12319.62309	1097.466249	1383.321519	92.947	8346.984589	16842.12209
13494	7898.95	10302.105	3864.95	18654.58	12311.79755	1078.824452	1373.250453	94.947	8370.348241	16833.19403
13593	7950.84	10314.052	3880.79	18688.32	12324.0039	1090.410344	1374.208613	92.842	8366.98779	16809.59325
13506	7866.58	10274.685	3839.79	18497.37	12335.9337	1101.41135	1379.472339	91.263	8345.203043	16783.03982
13280	7858.11	10204.053	3811.74	18517.21	12311.4561	1097.865882	1382.234887	92.368	8320.193589	16784.99144
13419	7845.05	10228.527	3826.79	18485.21	12341.17239	1090.512759	1375.991639	95.579	8335.677805	16789.15849
13431	7937	10291.263	3867.1	18644.47	12340.62259	1088.41376	1367.042143	92.579	8371.17206	16788.14157
13294	7828.26	10180.473	3829.42	18435.11	12276.80424	1092.03899	1345.953433	94.211	8300.165825	16663.00966
13285	7809.47	10173.579	3831.58	18434.52	12279.43453	1095.897711	1334.582477	92.526	8258.569457	16619.79465
13240	7837.32	10202.211	3822.68	18503.84	12267.66329	1098.395066	1346.455603	93.263	8267.054831	16653.66136
13118	7866.74	10263.475	3835.26	18525.53	12173.79762	1101.632759	1349.233408	93.421	8244.284332	16563.58999
13254	7794.79	10223.632	3808.89	18485.63	12154.91788	1095.880666	1342.620348	93.474	8246.929945	16512.77625
13230	7800.74	10168.158	3809.21	18386.42	12238.86921	1090.890508	1341.161105	94.158	8261.410047	16603.96486
13320	7838.79	10182.578	3812.53	18412.95	12218.38985	1095.142496	1341.2292	93.105	8232.611853	16592.41307

13102	7814.05	10236.894	3836.26	18496.37	12113.55718	1083.91863	1346.460645	97.105	8181.498566	16436.30212
13116	7825.53	10178.843	3807.05	18405.52	12165.6491	1082.151243	1342.063663	94.211	8240.768164	16509.21731
13184	7764.42	10143.842	3815.05	18283.37	12142.02156	1085.572644	1323.357765	92.263	8139.533127	16409.60298
13016	7803.68	10196.896	3805.11	18374.16	12194.70375	1097.222	1321.058597	94.158	8141.255052	16458.48946
13108	7785.68	10167.526	3824.11	18395.47	12148.60485	1096.794105	1340.607978	90.211	8176.837188	16442.75343
12949	7738.26	10112.842	3778.21	18268.58	12042.65764	1095.355042	1348.332341	90.316	8097.642651	16320.92256
13136	7774.26	10182.054	3785.47	18326.1	12109.17549	1090.667602	1321.097939	90	8116.571304	16339.98883
12855	7761	10131.526	3810.63	18304.63	12007.8912	1070.277784	1312.980454	89.632	8066.049955	16253.64011
12904	7753.63	10109.422	3772.1	18331.84	12127.94176	1085.90048	1334.279588	93.579	8100.238058	16361.92929
12852	7677.21	10051.841	3764.05	18141.58	11958.57629	1079.258503	1299.113044	90.211	8023.444776	16167.50764
12979	7788.58	10119.789	3803.42	18276.37	11910.1681	1062.853248	1292.412526	93.579	7986.140996	16101.38642
12874	7718.47	10112.895	3768	18230.95	11956.7391	1069.851856	1312.412135	93.684	8057.737795	16146.1861
12670	7703.47	10079.631	3769.74	18141.79	11978.18548	1088.320305	1304.873609	91.684	8035.19734	16179.73269
12870	7682.95	10041.053	3744.58	18130.47	11907.95759	1064.875355	1301.956482	93.421	8024.742853	16092.54296
12551	7596	9987.947	3706.42	18002.58	11922.89585	1071.191144	1301.572821	92.947	8074.350043	16081.74189
12714	7672.32	10073.736	3780.63	18078.21	12001.34732	1061.410585	1299.50589	93.526	8059.711845	16128.80701
12665	7699.26	10105.422	3793.26	18200.05	11816.32347	1061.946435	1282.938928	92.632	7939.104434	15913.35935
12547	7609.58	9984.895	3730.16	17970.89	11879.39943	1067.890997	1272.137974	89.947	7971.366359	16040.8092
12345	7566.58	9962	3702.47	17888.16	11779.23911	1064.860593	1270.031787	91.421	7911.3663	15853.14548
12707	7695.68	10125.474	3772.42	18201.21	11741.05851	1057.530015	1286.837612	89.947	7925.069646	15856.26907
12316	7598.74	9953.316	3739.53	17922.74	11781.12983	1056.522962	1269.956754	94.421	7947.709742	15911.30635
12334	7565.84	9889.055	3693.37	17845.63	11825.06308	1061.623346	1269.682676	90	7947.336566	15885.45089
12632	7630.95	10051.579	3752.74	18036.37	11640.09701	1052.699654	1258.817039	90.474	7911.332004	15780.13993
12513	7589.84	9969.579	3713.21	17909.74	11646.75181	1049.867666	1247.726466	90.526	7863.998462	15723.3314
12403	7619.68	9964.685	3741.58	17965.47	11788.98521	1046.81732	1262.130017	88.105	7838.817738	15774.78475
12429	7570.21	9942.315	3704.84	17879.42	11681.03794	1046.760195	1259.977161	89.158	7822.782198	15729.5631
12397	7563.53	9963.476	3716	17888.31	11616.94213	1048.627748	1260.469025	89.053	7822.154657	15646.45475
12213	7488.21	9856.737	3664.16	17681.89	11625.52598	1045.876958	1249.967504	87.316	7815.909486	15615.57823
12255	7564.68	10013.843	3710.74	17872.74	11622.2357	1047.304639	1242.686918	85.947	7782.259547	15616.20615
12383	7513.89	9903.843	3671.32	17694.95	11591.19281	1045.526307	1228.729836	89.789	7748.14712	15556.62444
12158	7448.42	9870.104	3673.26	17645.74	11614.54937	1043.529209	1235.062136	88.263	7749.296445	15565.55702
12244	7572.21	9951.159	3711.58	17843	11581.05927	1044.436896	1249.077473	92.684	7750.712658	15541.59004
12221	7492.05	9904.315	3693	17707.11	11520.08381	1040.612433	1245.849941	89	7759.997217	15506.39344
12240	7542.47	9922.474	3719.63	17751.26	11514.42162	1034.521901	1241.384197	90.053	7719.240096	15489.14273
12222	7424.9	9811.789	3667.16	17590.79	11451.75218	1028.75086	1222.564145	88.789	7631.726119	15365.51512
12048	7417	9773.579	3639.58	17531.53	11492.07238	1029.892343	1218.012513	85.105	7684.535684	15414.97421
12241	7520.89	9904.631	3718.79	17738.31	11546.05091	1038.186665	1228.54006	89	7748.539818	15475.86782

12040	7492.37	9867.368	3679.32	17723.63	11473.09344	1039.835591	1218.161833	90.316	7682.663238	15374.24167
12078	7481.47	9858.895	3698.32	17697.63	11466.30743	1035.633871	1214.680219	91.526	7638.327498	15325.43579
12090	7489.74	9856.843	3659.21	17603.53	11491.4537	1035.39772	1234.780766	92.947	7668.673452	15371.30248
11900	7394.47	9799.946	3638.89	17514	11442.07735	1039.642328	1221.871887	91.421	7640.83129	15329.73715
12103	7473.53	9830.316	3687.05	17646.63	11402.6912	1034.67607	1219.273762	92.789	7628.376253	15266.45681
11914	7456.84	9862.737	3680.63	17622.63	11390.71786	1037.041088	1216.551635	93.368	7615.572594	15303.51404
11878	7406.53	9858.263	3660.1	17550.05	11457.97929	1034.783463	1218.669985	91.684	7592.943865	15251.1889
11972	7440.37	9850	3652.32	17586.53	11340.10705	1029.813601	1192.533412	94.368	7602.488601	15171.30953
11921	7478.11	9905.842	3676.42	17670.47	11310.13294	1029.370401	1198.611968	90.211	7543.676711	15136.57255
11788	7380.05	9768.579	3642.32	17412	11249.39087	1014.694259	1195.181144	89.474	7513.871517	15064.40229
11981	7452.32	9867.21	3676.89	17542.11	11265.83611	1018.283552	1184.361428	86.316	7586.787158	15132.31109
11841	7385.84	9796.685	3629	17424.95	11211.53374	1017.208761	1170.857608	89.474	7451.796311	14999.07227
11638	7403.11	9779.369	3621.37	17445.42	11411.51836	1039.573402	1191.277497	89.105	7592.567181	15209.4726
11805	7400.16	9875.21	3658.89	17543	11158.75819	1006.086342	1165.808265	94.579	7445.537706	14960.71721
11723	7377.42	9759.999	3639.47	17424.31	11235.5579	1029.143072	1184.109085	88.947	7510.948208	15028.05879
11627	7325.53	9750.79	3617.53	17326.42	11180.39226	1015.343368	1162.613294	84.895	7418.620835	14892.9921
11673	7351.16	9771.527	3638.32	17407.37	11311.80675	1016.942075	1171.031742	89.684	7468.014886	15009.70339
11531	7339.47	9758.896	3633.37	17331.84	11187.46818	1012.290406	1166.482013	90.526	7388.882662	14875.59627
11635	7330.79	9740.579	3634.84	17360.21	11068.60596	1002.364571	1151.020202	90.632	7311.960726	14725.28827
11729	7349.63	9765.315	3652.16	17344.42	11074.48227	1003.835653	1152.155331	89.105	7326.21882	14738.20348
11654	7305.16	9677.999	3609.26	17238.79	11092.13839	1004.017937	1158.315974	87.947	7302.591241	14699.02418
11749	7382.95	9828.578	3648.63	17443	11014.02986	992.0543522	1151.177597	89.789	7294.21496	14570.68193
11536	7315.79	9771.842	3628.26	17284.26	11038.36901	991.0666646	1158.964095	89.842	7264.276236	14579.36974
11564	7268.26	9720.947	3594.95	17195.74	11098.9985	1003.805897	1159.191509	89	7305.32993	14661.71865
11539	7283.1	9724.368	3619.26	17253.05	11079.37312	1006.913285	1145.854472	92.053	7296.26664	14636.8131
11353	7262.63	9690.685	3588.9	17175.21	11027.69619	996.3378761	1138.741223	87.684	7239.418915	14535.46126
11453	7292	9685.789	3589.84	17210.11	11046.17436	1008.430549	1127.215381	89.579	7278.051203	14563.13484
11328	7263.42	9699.842	3619.26	17212	11037.97434	1008.910576	1125.002465	90.632	7272.817519	14540.70163
11507	7290.42	9653.263	3616.84	17177.47	10974.13693	1003.893154	1135.588497	89.684	7227.473956	14494.23966
11476	7271.16	9716.474	3594.37	17195.11	10864.5552	995.0707707	1125.152552	88.211	7205.697941	14408.89584
11291	7224.68	9605.947	3570.16	17035.42	10742.30849	977.8563304	1102.631119	85.368	7121.418088	14269.01872
11462	7281.95	9746.947	3592.42	17214.79	10766.37077	981.1568039	1104.774199	92.211	7089.032942	14270.23853
11207	7203.63	9601.789	3558.53	17014.26	10759.50233	985.8944033	1105.501942	89.947	7101.362937	14250.78658
11364	7259	9699.264	3593.68	17143.26	10694.51774	981.9811796	1097.115913	91.789	7046.048408	14196.41495
11212	7198.21	9635.789	3573.79	17052.58	10749.23744	984.2200718	1105.739912	94.158	7047.40482	14225.1457
11216	7156.21	9605.053	3576.11	16940.58	10662.04248	975.214648	1094.093523	90.316	7046.24036	14134.6096
11425	7277.58	9768.579	3594.74	17183.16	10654.16147	975.6293893	1079.759221	93.947	7033.652845	14167.99245

11173	7163.21	9570.368	3565.63	16901.74	10709.85084	982.4835221	1092.472483	89.842	7050.311766	14166.03161
11222	7196.63	9649.526	3560.47	16993.42	10708.0493	980.4059582	1089.756433	94.947	7040.602099	14108.81499
11006	7148.26	9617.369	3537.47	16928.68	10640.82848	968.7988646	1080.255013	90.842	7013.99973	14028.3385
11154	7178.37	9594.684	3581.74	16962	10646.70809	961.8079645	1091.551963	90.474	7041.701534	14098.53031
11147	7216.53	9661.526	3572.16	17033.21	10566.63258	965.8707023	1085.966963	94.474	6989.344513	14015.4401
10962	7109.05	9531.789	3538.47	16795.37	10551.85061	967.6427395	1073.690024	88.632	7011.807492	13956.87749
11067	7143.11	9541.736	3567.74	16856.63	10527.89246	966.1323804	1073.770032	85.789	6954.383579	13889.09093
10983	7108.63	9549.369	3564.74	16827.89	10613.53437	981.8506092	1089.102624	91	6992.931442	13999.5382
10900	7094.89	9510.474	3552.26	16775.53	10589.11478	972.2335841	1070.428563	86.316	6992.879719	13966.44688
11059	7194.05	9658.001	3589.58	16989.9	10458.78528	960.2965138	1060.08653	89.421	6935.216372	13806.04851
10865	7104.58	9534.526	3546.53	16738.42	10440.84505	959.4541358	1069.802142	87.421	6898.596128	13822.45092
10907	7070.05	9469.315	3519.53	16679.42	10445.92577	960.2109428	1063.316754	89.158	6849.727484	13753.16906
10968	7121.37	9533.421	3538.47	16840.21	10508.04174	971.2900395	1054.495719	87.842	6997.912764	13822.53908
10808	7056.68	9508.685	3526.79	16747.21	10521.31932	969.9177001	1051.114057	87.053	6869.163367	13803.6831
10832	7071.32	9474.158	3539.63	16688.58	10548.18295	965.1653881	1064.726836	85.842	7000.881065	13877.66921
10853	7120.05	9575.37	3554.95	16782.63	10537.19668	960.6809495	1061.069706	88.158	6962.232665	13877.1137
10692	7006.68	9483.212	3521.74	16618.16	10480.17564	965.663161	1052.617054	86.632	6940.52631	13849.43322
10855	7085.68	9493.946	3555.63	16653.74	10418.13368	955.8296735	1042.024656	87.368	6828.814866	13687.75446
10631	7017.79	9465.526	3497.79	16582.47	10434.21137	952.5640564	1044.928001	84.263	6835.238572	13705.24718
10680	7013.53	9411.948	3510.37	16600.63	10473.6172	960.397884	1047.919629	83.632	6831.216581	13720.69598
10706	7049.16	9465.21	3517.84	16581.58	10504.83683	955.0308784	1049.590268	86.579	6873.349424	13720.75858
10867	7037	9501.157	3523.53	16602.69	10464.72101	965.2164215	1050.472743	87.105	6930.497523	13727.72091
10617	7036.95	9500.262	3542.63	16598.16	10343.65791	954.7317213	1047.941378	88.842	6833.495796	13545.8709
10479	6971.47	9377.999	3485.58	16407.37	10351.11803	946.6794878	1043.834678	84.789	6782.209836	13554.80317
10737	7023.1	9499.475	3531.74	16660.47	10319.0944	940.7701081	1021.678699	83.421	6712.535858	13503.94186
10617	6943.74	9390.631	3494.26	16424.31	10348.28056	950.1379846	1027.741476	83.842	6760.085153	13578.36802
10596	6975.74	9415.946	3509.89	16434.16	10308.30666	945.2250205	1036.306548	82.895	6784.991676	13534.50521
10716	6933.05	9371.684	3494.68	16433.26	10256.52441	940.4206006	1023.488906	83.316	6720.652432	13430.80681
10367	6954.95	9392.422	3519.58	16435.47	10184.7638	938.3057825	1009.901819	83.842	6670.32977	13324.37836
10253	6902.95	9277.158	3454.05	16277.21	10223.81992	936.5008974	1004.891716	79.053	6696.629603	13344.8427
10554	6985.84	9427.791	3507.68	16478	10276.5249	937.892768	1007.587517	82.789	6719.996494	13401.70032
10513	7021.21	9472.104	3523.1	16515.63	10222.27784	943.4295235	1014.875613	84.368	6709.67273	13373.49601
10326	6906.63	9378.212	3463.47	16346	10189.89579	942.4532372	1016.246014	78.632	6690.618578	13358.09301
10345	6954.58	9376.105	3497.26	16336.32	10126.95695	926.2245383	1011.77029	81.789	6646.481529	13274.44047
10222	6893.16	9257.527	3441.37	16179.95	10172.85636	933.4946577	1009.124872	82.526	6676.250876	13315.32449
10413	6955.47	9428.843	3508.37	16410.42	10146.7819	937.5397273	995.9419159	84.211	6661.232109	13250.78506
10314	6888.89	9281.368	3473.79	16236.63	10096.5428	934.6875418	986.3787316	82.053	6587.928031	13164.5975

10174	6869.58	9315.525	3473.26	16243.79	10014.34685	928.2390032	985.8673052	81.895	6548.043577	13100.97325
10363	6909.26	9370.104	3449.05	16310.74	10111.72641	934.5372364	984.544002	80.368	6608.771963	13207.51346
10151	6886.58	9343.999	3483.63	16255.84	10091.06673	933.1474467	984.4742786	82.474	6583.866487	13140.17841
10219	6872.68	9310.79	3482.42	16156.58	10079.41883	935.2874824	985.5039372	80.316	6561.085011	13132.90341
10238	6903	9316.579	3458.74	16167.53	9987.673062	926.9626598	973.4936827	83.947	6506.606139	13000.37702
10112	6839.58	9307.842	3450.32	16142.95	9975.935749	932.9625093	974.8877229	83.158	6520.016978	13041.69813
10120	6866.84	9311.736	3470.95	16195.1	10017.75448	925.3209582	962.7573891	79.737	6491.877934	12988.42178
10040	6851.9	9254.631	3454.84	16064.95	9965.246154	920.8593923	968.9508477	81.737	6455.126069	12941.32256
10094	6859.47	9280.475	3467.32	16176.95	9916.5053	927.9848464	961.5120632	83.737	6487.884643	12919.82755
10151	6842.84	9255.264	3462.05	16054.42	9811.744665	906.9417695	967.6843639	82.158	6469.986474	12789.09513
9991	6801.21	9248.315	3428.26	16020.26	9946.797925	934.8168635	968.6567395	84.632	6497.703018	12853.38149
10019	6874.05	9381.579	3480.26	16183.79	9716.875339	905.0841594	946.6541772	82.105	6334.030965	12665.14416
9959	6785.16	9222.422	3419.42	15934.79	9842.43742	927.7692546	948.9962977	83.526	6400.368033	12814.46988
9951	6832.42	9265.159	3441.58	16013.53	9850.277293	930.2498536	951.9414159	82.368	6418.868238	12797.7021
9963	6741.84	9169.316	3422.21	15895.47	9845.521657	907.8740478	943.6286275	80.579	6381.581413	12742.3101
9788	6773.11	9206.685	3424.42	15916.47	9816.32732	912.7219195	946.9841121	83.526	6395.609048	12688.53233
9766	6802.84	9248.632	3451.79	15985.74	9834.485193	907.0651101	957.477526	84.895	6411.351862	12723.22799
9832	6745.63	9215.842	3421.84	15895.26	9705.544333	908.4740434	935.0572853	86	6353.904429	12632.5613
9761	6709.9	9138.736	3412.42	15786.68	9691.794671	902.8200979	922.3753296	85.684	6309.504849	12550.41868
9681	6739.05	9216.317	3444.26	15891.26	9692.239373	895.9505789	931.8022944	77.632	6265.756943	12500.07008
9672	6695.11	9060.368	3407.05	15694.95	9643.421657	893.905558	935.8571105	78.368	6268.466898	12471.53065
9683	6650.32	9094.737	3384.95	15729.68	9628.896343	902.4586854	916.9273293	82.158	6285.120906	12447.05076
9596	6703.63	9078.946	3408.53	15680.05	9604.444702	898.4815193	905.6651436	80.737	6249.080871	12406.67599
9587	6684.53	9051.685	3380	15635.53	9627.686768	891.8835746	919.7292983	78.632	6190.589101	12368.42566
9505	6614.74	8988.895	3359.26	15499.95	9614.793447	888.9057548	924.5636297	82.211	6185.905899	12333.36862
9374	6606.26	8993.79	3356.63	15493.63	9605.42379	893.1878287	907.9241657	79.684	6220.372486	12366.59424
9590	6652.84	9007.526	3385.26	15521.52	9573.311351	891.0920501	906.7862562	79.579	6200.441967	12322.3846
9404	6624.89	9024.631	3377.95	15514.53	9541.329436	882.9949779	910.4094088	77.211	6170.009549	12283.87729
9472	6639.11	8976.264	3384.68	15477.89	9555.691453	887.7600829	900.2215028	78.895	6166.071332	12289.24142
9427	6572.63	8886.684	3342.37	15347.42	9521.440808	899.2230797	894.2172827	79.789	6194.442518	12269.41618
9449	6628.1	9007.211	3381.84	15459.74	9460.080094	901.005337	898.6027127	77.737	6172.376886	12227.69347
9334	6558.84	8923.685	3359.26	15332.53	9423.586486	889.4679893	896.893648	79.737	6095.510437	12136.51904
9482	6635.05	9072.633	3395.58	15514.58	9380.422281	877.32282	887.2116332	80.526	6099.963385	12087.68565
9342	6547.53	8910.685	3341.79	15355.53	9379.546842	879.9429984	887.7201634	75.684	6090.027854	12090.71802
9249	6540.47	8876.632	3320.26	15299.84	9339.487728	872.860852	883.5766882	79.105	6041.139473	12039.76924
9139	6510.21	8926.527	3341.16	15296.53	9274.66949	855.2778271	871.3694903	82.263	6006.303231	11947.95352
9192	6565.74	8938.315	3361.84	15318.58	9402.496841	872.3822245	882.8087778	81.789	6042.689399	11995.81375

9158	6505.68	8907.104	3340.63	15302.79	9406.316575	875.9088197	887.8033883	79.947	6079.677122	12022.72975
9107	6464.42	8779.841	3291.21	15105.63	9244.792772	857.4627383	861.0818859	81.789	6001.763675	11864.49131
9218	6511.74	8888.526	3323.11	15229.21	9279.386763	862.423442	880.1110616	82.474	5999.555701	11896.0444
9005	6444.21	8733.104	3279.1	15000.84	9302.416868	867.3060994	883.2233283	84.789	6008.830575	11922.65871
8934	6382	8724.368	3283.42	15005.42	9192.098074	858.5647177	858.4499187	82.421	5941.53844	11775.63664
9002	6478.63	8814.528	3313.16	15121.79	9205.436979	878.2428421	841.4959684	81.579	5944.973366	11807.38451
9105	6495.11	8840.842	3344.58	15139.9	9273.749446	868.9575848	869.3017261	81.211	5992.220234	11834.0595
9046	6481.1	8785.684	3306.53	14973.1	9093.664824	848.0466897	842.7584374	81.737	5893.832038	11681.05884
8899	6434.9	8772.843	3292.95	14971.58	9271.167245	867.9630671	855.0817269	80.789	5980.082851	11797.31147
8957	6463.68	8765.632	3324.79	15003.9	9126.715002	840.9533875	838.5513402	78.789	5822.779305	11629.13366
8854	6415.32	8781.263	3318.95	15058.1	9116.760872	851.5117612	857.0143439	81.158	5864.725968	11632.66202
8943	6503.84	8865.685	3340.53	15118.74	9142.303577	856.0594152	847.4483567	78.579	5900.496578	11682.84545
9081	6521.63	8932.422	3370.79	15243.74	9062.97277	861.9985331	848.6998931	81.947	5869.293606	11558.08902
9015	6507.63	8904.157	3367.89	15172.58	9146.552735	858.336345	848.0058575	82.421	5922.946301	11625.24771
8954	6515.63	8979.526	3350.47	15228.32	9000.650455	857.3974495	845.2285671	82.632	5830.037027	11484.49074
8888	6448.37	8849.895	3324.95	15084.58	9119.720702	860.0001788	847.0769211	83.684	5901.337158	11657.43123
8996	6482.53	8922.632	3377.26	15143.32	9066.038799	865.2654702	846.6665756	84.842	5865.175252	11555.22582
8894	6432.26	8866.368	3356.58	15072.95	9043.970528	852.5426582	828.3382747	82.789	5833.740772	11503.21274
8922	6497	8878.737	3350.21	15144.32	8970.771013	856.8841176	830.8607624	84.053	5806.16048	11465.61453
8961	6484	8933.895	3372.11	15210.95	8948.326426	845.1998144	833.2369633	88.211	5809.968261	11453.67668
8835	6508.84	8937.738	3393.16	15160.84	8992.077278	847.2579298	838.7029167	92.158	5818.118702	11485.83399
8814	6468.74	8886.58	3371.95	15098.58	8927.995322	846.8829866	822.9235722	93.053	5758.405867	11337.33529
8712	6393.53	8793.158	3335.63	14921.05	8900.61975	844.4661015	814.9648164	90.158	5751.088299	11325.87352
8833	6518.53	8935.263	3398.21	15140.21	8916.381459	837.4197143	818.8087814	92.368	5731.062978	11316.45083
8745	6424.26	8878.578	3320.53	15003.11	8893.891227	832.421468	820.9706511	87.579	5691.210246	11267.31629
8638	6470.89	8892.474	3361.37	15037.21	8930.335815	835.1209889	820.4991386	89.684	5700.41343	11303.10176
8770	6432.21	8813.632	3350.32	14971.58	8887.443777	839.003989	813.139232	88.158	5707.252177	11260.68567
8589	6354.11	8722.947	3329	14777.79	8833.157002	829.5380695	800.4454325	86.737	5693.40643	11186.93014
8733	6501.63	8929.789	3372.58	15086.37	8840.358505	822.2014157	799.1389289	86.105	5702.730909	11171.07068
8631	6389.1	8805.316	3336.95	14865.84	8802.278212	828.7178058	797.7706796	83.421	5710.015056	11166.49262
8636	6363.95	8783.737	3327.47	14826.95	8829.291427	835.7851627	792.8905101	85	5695.035614	11180.73439
8555	6449.74	8901.684	3366.16	14978.42	8828.510794	830.2919519	792.9311523	87.632	5639.231627	11109.00802
8568	6426.9	8813.315	3354.89	14885.11	8747.880571	814.0955714	789.8332857	87	5592.133694	11026.11426
8534	6382.74	8828.842	3329.9	14862.32	8785.20248	820.1098504	802.4065116	89.053	5642.781272	11060.48143
8676	6373.63	8829.211	3349.79	14854	8776.178862	826.171807	799.7716294	86.947	5637.400829	11053.39282
8457	6306.53	8723.842	3310.84	14701.26	8780.089225	823.2989661	792.6322403	88.368	5617.872765	11042.69068
8543	6390.21	8829.632	3381.11	14861.58	8698.147306	826.516049	786.4735685	91.842	5574.315457	10939.54548

8479	6380.16	8815.737	3359.21	14823.32	8681.848693	835.4293607	775.5720549	92.737	5583.511845	10946.91541
8245	6309.58	8641.736	3324.37	14573.95	8672.876584	814.5518962	783.9812841	92.211	5537.013117	10911.28474
8432	6354.42	8757.999	3350.42	14736.16	8656.769267	823.644148	781.8372365	94.632	5602.177405	10901.93299
8256	6358.42	8725.946	3337.95	14670.58	8652.663665	813.789777	761.9089357	97.684	5515.029224	10868.48256
8341	6353.21	8778.791	3339.89	14696.47	8645.970294	806.3512636	764.3571531	97.211	5527.910365	10810.45188
8426	6393.84	8772	3370.68	14738.84	8643.515416	807.5276309	772.0052953	97.368	5551.402036	10812.08663
8225	6336.84	8753.736	3337.68	14663.95	8517.098384	799.4317577	772.5750592	96.211	5517.997074	10742.70643
8249	6314.05	8691.369	3329.26	14553.84	8577.11355	818.5609637	758.6772723	100.474	5450.669985	10743.0177
8287	6347.42	8813.105	3363.79	14741.63	8521.57923	797.3845659	746.2522557	104.368	5457.23443	10695.76832
8272	6304.53	8724.526	3332.21	14587.95	8522.845644	809.61994	762.4965938	102.368	5548.654494	10723.2797
8179	6329.95	8779.263	3344.05	14652.95	8515.244384	811.9893717	751.4821878	101	5426.642695	10640.49869
8229	6294.47	8680.422	3325.74	14542.42	8491.503636	825.9334189	754.2329187	98.263	5440.489221	10668.2048
7989	6288.05	8691.578	3338.84	14493.32	8463.704671	803.565659	745.7830095	96.158	5420.991578	10577.07568
7923	6233.16	8618.421	3281.89	14439.16	8486.21834	811.915232	757.5537403	93.263	5388.182869	10609.44506
8065	6329.79	8770.105	3359.05	14572.79	8442.197778	794.4614765	756.1542242	92.158	5372.647467	10550.342
8177	6234.53	8600.053	3319.42	14357.26	8372.600699	789.9305912	735.8834945	86.684	5354.426263	10468.97082
8017	6241.21	8631.58	3310.21	14408.58	8442.352785	787.7939227	740.8575083	86.947	5374.368064	10544.82748
8028	6218.79	8572.999	3304.68	14366.79	8394.438957	789.7188804	744.9146913	89.474	5336.140372	10494.21079
8043	6265.89	8633.105	3339.42	14379.79	8387.126715	805.0559199	745.7338729	83.789	5364.24939	10473.69424
7931	6237.68	8611.21	3329.37	14331.74	8292.049749	793.486674	738.3388923	83.632	5282.199976	10348.45862
7977	6228.42	8672.737	3319.63	14372.58	8226.772502	790.4744141	725.976938	83.211	5260.792546	10282.10982
7940	6224.05	8626.421	3318.05	14329.37	8300.716213	787.2474006	724.9185718	81.737	5287.948987	10324.45367
7814	6197.32	8609.316	3302.42	14300.47	8298.144091	789.3987593	720.11015	83.421	5282.358197	10301.04511
7938	6236	8615.737	3325.11	14332.37	8345.765932	804.7555681	721.9284856	81.105	5323.393641	10362.35138
7891	6214.26	8645.473	3322.26	14309.63	8304.803022	798.7836188	716.5925383	80.421	5339.25341	10324.70064
7874	6246.58	8689.842	3329.21	14363.1	8224.529838	786.993955	711.8243331	80.789	5289.25847	10233.28764
7880	6218.47	8596.422	3321	14243.74	8261.207454	789.8323375	722.2194734	85.579	5290.357539	10279.83219
7809	6227.84	8591.526	3326.89	14207.58	8221.613767	791.8864278	720.7641902	81.368	5293.557716	10215.79479
7781	6235.21	8645.368	3339.11	14317.63	8164.290043	798.4923883	712.4813978	81.789	5262.444348	10130.40385
7742	6179.63	8582.158	3321.37	14235.16	8167.642389	800.7807679	716.7861674	78.105	5243.426222	10159.95274
7777	6182.84	8529.947	3316.32	14135.69	8134.625657	786.2136575	717.8011855	79.368	5219.69525	10115.70454
7755	6207.37	8626	3333.74	14232.42	8163.110133	780.7471204	710.5259874	81.947	5215.750588	10109.33146
7533	6091.26	8455.105	3259.95	13954.68	8157.158282	779.5491949	698.8463465	76.947	5190.243408	10074.31263
7672	6221.37	8702.368	3349.89	14273.89	8120.648637	772.491526	694.1500391	82.632	5170.081416	10006.19668
7533	6098.74	8443.368	3278.95	13947.42	8078.46629	771.5442767	695.5925578	83.737	5153.890126	9985.886704
7615	6161.42	8596.053	3334.05	14179.32	8003.488436	766.3369203	687.4723291	81.895	5135.627901	9901.469783
7495	6119.58	8506.63	3280.05	14001.89	8051.480601	768.2638548	686.7989112	79.211	5130.411717	9936.826909

7599	6153.63	8555.105	3316.32	14057.58	8010.167391	760.4535697	684.1074477	79.789	5085.897399	9887.00692
7416	6070.84	8436.052	3265.37	13977	7949.332263	763.1320549	686.5238863	79	5072.517029	9858.119682
7467	6088.05	8488.895	3305.26	13964.47	7939.396033	765.2313915	675.5464684	83.211	5085.695372	9795.542902
7397	6007.16	8363.052	3234.37	13762.95	7892.447574	768.2798535	673.8053628	83.579	5061.77233	9747.424504
7525	6118.1	8480.316	3303.89	14036.26	7949.95921	775.2123311	677.2609227	83.368	5082.278837	9781.203951
7391	6070.84	8374.264	3261.42	13740.37	7952.44169	767.513532	682.8966511	81.053	5083.092897	9794.446577
7402	6102.68	8479.157	3294.74	13925.1	7935.733598	740.8182282	669.773428	88	4998.722215	9699.142145
7386	6037.11	8420.947	3278.84	13795.37	7749.847478	734.7937853	658.58985	87.158	4906.600645	9505.94399
7428	6075.79	8446.104	3299	13889.21	7861.022108	744.5175422	679.4414743	82.526	4978.809537	9588.371838
7277	6032.58	8426.896	3268.11	13783.42	7899.540366	761.7068958	671.5880734	85.684	5005.119186	9660.259237
7232	6025.16	8386.579	3256.53	13731.26	7872.97423	759.6041425	659.4741627	87.105	5047.143262	9647.072316
7352	6147.47	8558.895	3335.37	14025.74	7793.118639	747.6500331	671.7113094	86.789	4956.303775	9574.394275
7230	6050.53	8383.157	3288	13780.89	7808.215946	745.7430004	667.5798264	92.421	4939.355514	9559.55744
7273	6061.68	8431.789	3276.63	13825.63	7831.983888	756.5319822	666.9453107	96.684	4973.805287	9599.878372
7233	6049.37	8438	3291.32	13765.84	7722.436408	745.9213149	650.3049136	104.158	4941.776365	9489.096208
7215	6006.11	8404.738	3258.21	13713.37	7775.402279	751.3012013	666.8866194	116.632	4929.574047	9495.42022
7280	6032.16	8394.368	3274.84	13762.37	7872.894907	751.5763741	668.8206397	128	4984.613451	9589.74881
7048	5985.79	8322.42	3237.89	13633.58	7749.265009	742.5920525	645.1633035	138.737	4905.322415	9448.589077
7087	5995.58	8361.736	3252.89	13669.47	7687.574131	752.6208113	645.5801303	144.684	4933.107304	9421.72185
7086	6064.32	8445.685	3299.68	13811.37	7673.316882	740.4749882	650.5603769	158	4908.526402	9404.951759
7061	5998.58	8380.053	3276.05	13661.37	7695.481536	747.6474274	651.1822695	154.842	4896.463855	9391.878218
6941	5972.89	8343.37	3238.95	13582.74	7647.770804	735.6012933	645.1472728	160.053	4885.365442	9312.187205
7107	6065.53	8448.631	3304.74	13795.68	7607.543455	730.9857411	640.2902222	161.474	4844.901187	9270.951891
6949	5962.21	8319.527	3244.89	13534.74	7604.241918	734.0199179	645.0814175	153.158	4839.417396	9264.477715
7063	5937.74	8335.631	3254.84	13571.74	7641.270526	725.9397248	635.0971173	151.158	4854.586061	9254.011328
6981	5968.47	8325.736	3264	13607	7649.535337	731.4635856	624.179232	147.947	4844.032788	9256.030548
7067	5986.74	8446.685	3274.79	13665.63	7614.983439	736.6537987	623.7206748	151.526	4804.80171	9225.336977
7054	5972.47	8359.526	3276.26	13540.68	7576.366004	730.3409574	627.7117319	151.842	4778.293618	9186.51702
6944	5881.74	8276.263	3219.47	13419.37	7514.204221	728.9657285	630.5078548	151.737	4759.579119	9121.634475
7030	5974.42	8336	3234.26	13488.63	7514.077214	728.3494254	626.0452139	156.895	4756.493501	9075.989896
6928	5921.58	8332.263	3258.16	13539.32	7543.354107	729.1731098	626.0746988	153.211	4773.337076	9121.344575
6804	5896.95	8322.526	3242	13484.84	7483.474349	727.9026401	618.8812155	156.474	4738.733676	9079.706569
6839	5934.74	8288.421	3243.68	13444.84	7460.473005	725.3733607	619.2234657	158.421	4742.417341	9041.408129
6832	5927.32	8277.053	3252.53	13427.84	7462.003253	727.4126676	620.0604785	155.737	4727.820571	9033.728651
6813	5932.05	8355.263	3248.53	13488.68	7419.13588	724.6180947	615.894783	159.053	4728.763194	9021.624857
6755	5917.74	8237.842	3239.74	13389.26	7414.062446	719.6936384	626.1858772	156.526	4743.366512	8989.963301
6891	5903.95	8278.632	3215.58	13426	7523.403798	725.0522226	637.8069558	159.474	4762.965676	9089.931572

6692	5911.58	8312.843	3215.47	13440.32	7393.783225	706.1757727	617.187294	160.263	4673.958043	8929.407285
6650	5862.58	8228.317	3202.21	13292.42	7366.791081	713.2596542	605.5903143	163.684	4685.21331	8904.525793
6770	5908.32	8322.736	3222.89	13478.47	7403.898936	726.512427	606.9889274	162.211	4702.351092	8934.812656
6681	5864.05	8228.104	3216.74	13307.31	7291.28597	715.2713686	601.9767167	161.526	4645.708159	8828.174793
6730	5857.58	8232.895	3218.84	13321	7361.845978	715.7441966	611.5946632	163.895	4676.91897	8903.383401
6632	5872.37	8292.789	3221.89	13367.95	7332.976494	715.1101985	605.5305395	165.895	4612.081045	8818.31961
6617	5813.32	8211.264	3180.58	13226.58	7360.220271	711.8012155	611.1256243	167.474	4671.949293	8867.703933
6659	5800.68	8167.263	3185.63	13178.26	7203.451917	696.3511381	594.1635028	167.421	4572.996367	8697.114794
6669	5860.63	8257.999	3202	13326.37	7248.583266	699.3795657	604.44621	164.947	4651.299198	8759.804056
6608	5843.74	8220.526	3215.42	13259.79	7215.538155	694.4296685	598.8486796	161.474	4580.542922	8731.46458
6651	5803.1	8236.211	3202.42	13251.53	7224.091116	697.3814144	602.2120497	150.789	4613.632595	8684.379265
6276	5765.9	8145.474	3169.58	13123.26	7161.646	695.7536028	594.2823182	146.158	4574.024094	8583.393115
6573	5818.84	8236.948	3199.21	13204	7194.344028	703.7485746	599.064884	147.632	4540.380081	8609.811459
6540	5820.84	8217.264	3184.74	13201.21	7185.668167	703.258953	594.4495742	150.316	4548.44176	8614.407462
6414	5730.74	8073.42	3135.74	13032.32	7197.204902	705.131336	586.4000703	155.684	4569.343074	8619.144473
6565	5848.16	8308.737	3223.95	13277.47	7128.650956	698.2128856	583.0429771	171.789	4528.864406	8523.859766
6453	5741.21	8053.947	3149.47	12979.53	7134.134766	697.8837549	590.7355714	182	4511.516487	8540.095796
6424	5779.16	8144.948	3181.47	13113.47	7135.145315	705.9160095	588.7893514	207.368	4532.069502	8542.437015
6285	5717.1	8084.842	3151	12959.9	7136.164787	701.5152024	582.3253998	231.263	4523.905756	8504.481724
6458	5837.58	8273.315	3205.16	13281.21	7110.662215	687.0458946	587.6185515	260.789	4512.108116	8486.968883
6385	5716.47	8133.631	3160.1	13045.32	7078.362289	680.3553275	583.6965726	287.895	4491.240693	8432.006172
6266	5722.63	8033.895	3119.42	12963.79	7069.332831	685.6655059	573.8551504	294	4455.429009	8406.690654
6415	5811.16	8255	3214.89	13229	7057.44777	693.0448129	566.9416451	310.632	4465.343	8395.913226
6212	5677.63	8034.263	3134	12890.05	7023.108431	689.4191235	568.0895036	299.421	4434.876449	8361.417177
6362	5741.21	8125.842	3165.74	12978	6990.722379	682.8160071	566.5948564	308.158	4407.118686	8326.262678
6231	5729.32	8054.105	3155.26	12910	7023.357174	696.015608	561.6753719	318.947	4419.050428	8347.89038
6329	5748.84	8152.21	3177.95	13015	7004.318787	694.3048303	562.1483141	350.158	4401.831079	8323.936603
6304	5678.58	8028.263	3096.89	12826.16	6945.972147	679.5777096	564.5099669	357.789	4393.611666	8266.618558
6170	5692.21	8047.368	3145.32	12916.47	6944.818786	685.1529818	556.2739889	369.105	4387.565047	8268.515332
6241	5687.74	8111	3149.42	12915.53	6912.738683	681.9851271	552.4870474	392	4388.855808	8231.543141
6121	5607.37	7959.42	3097.79	12751.95	6910.448724	679.565974	564.9963725	409.684	4405.523497	8208.985437
6234	5671.42	8111.842	3140.89	12893.63	6869.721674	674.7007426	554.4069704	436.579	4366.297845	8173.161731
6168	5627.84	7992.947	3120.42	12747.26	6878.545302	677.4812463	559.48106	457.263	4368.236021	8171.078246
6208	5710.26	8126.052	3176.89	13025.11	6869.169251	670.2440533	551.3721851	496.316	4325.521184	8111.439702
6167	5619.84	7989.685	3116	12735.84	6918.118587	678.4113443	556.5547813	506	4348.023411	8178.747925
6008	5607.84	7907.685	3069.68	12671.1	6815.015059	682.3431744	554.9880296	524.895	4295.752442	8099.083057
6035	5639.42	8015.053	3137.16	12766.74	6854.301175	677.9281066	556.0144807	542.368	4327.386046	8102.347443

6091	5652.32	8044.21	3141.53	12806.89	6854.14884	670.3296936	550.455803	565.895	4337.430345	8051.362981
5910	5513.16	7825.895	3022.84	12503.32	6782.565732	665.3717005	558.6800036	577.474	4263.713037	8008.272034
5977	5622.63	7975.948	3108.05	12702.53	6783.868538	671.0856609	547.727229	612.105	4316.708637	8038.68989
6001	5578.21	7950.421	3101.95	12669.95	6758.815047	668.232882	543.091571	618.105	4312.379151	8011.753248
5894	5594.95	7986.737	3117.37	12648.32	6686.735309	662.5373461	546.0291673	629.684	4224.141974	7888.869099
5933	5606.1	7984.895	3110.47	12714.11	6787.089619	676.0224402	546.6800861	621.947	4317.398704	7965.329719
5936	5528.16	7919.895	3072.05	12548.48	6659.333214	644.1382996	536.6275886	634.895	4255.644299	7861.036059
5884	5579.63	7971.158	3092.79	12610.32	6747.651144	658.2930134	544.8201657	636.526	4286.462189	7949.149976
5857	5536.47	7930.21	3078.21	12570.79	6674.680934	660.8531965	543.6782873	626.211	4245.144495	7912.07338
5698	5524.05	7857.684	3066	12482.05	6636.579463	656.6031812	535.1616644	636	4242.649116	7831.747833
5849	5551.42	7889.21	3069	12552.9	6628.836691	647.3007837	532.6727403	630.316	4245.581502	7788.76468
5908	5620.74	8027.105	3123.53	12740.89	6680.814775	667.9368587	541.6313252	638.474	4295.147961	7865.416231
5793	5485.32	7835.79	3056.95	12425.58	6530.070138	655.3171149	539.887728	616.368	4214.913607	7709.587392
5841	5502.68	7870.736	3050.79	12460.47	6527.88102	642.8827561	534.4676606	612.421	4223.919608	7680.786847
5785	5498.26	7880.421	3054.74	12508.79	6533.958169	651.0328268	526.0402368	626.053	4218.821782	7703.185518
5760	5512.95	7878.631	3078.84	12482.31	6555.07506	652.052255	529.5616056	624.526	4206.870317	7686.715918
5670	5454.37	7814.263	3045.84	12376.42	6530.436544	650.6740525	530.0210418	631.158	4225.153282	7649.246797
5740	5492.21	7831.368	3044.11	12381.21	6539.1383	651.1977968	527.0746097	642.211	4261.951814	7647.361594
5718	5475.26	7867.052	3045.16	12431.53	6526.298009	646.5707852	524.1215227	672.526	4275.412533	7640.954449
5663	5448.95	7806.632	3036.47	12329.74	6492.922044	647.2769984	517.0257964	723.789	4232.876169	7598.40776
5617	5488	7839.58	3052.11	12409.74	6490.909962	643.449572	511.9449893	772.947	4231.979754	7575.763704
5613	5457	7805.369	3047.53	12342.53	6493.259566	643.8548074	515.03256	804.474	4259.91228	7566.265783
5703	5477.21	7825.526	3046.68	12338.58	6488.117251	646.6226563	520.8681969	841.947	4250.989776	7545.754193
5510	5381.37	7730.631	3024.05	12209.21	6464.88821	640.5396838	520.379805	866.421	4226.147921	7521.543218
5585	5449.95	7768.737	3025.68	12257.16	6437.378734	634.6840375	518.6354294	919.263	4213.111944	7501.403988
5565	5497	7853.737	3066.47	12368.37	6398.561392	636.9494499	512.0129479	942.053	4200.035435	7481.031006
5390	5390.32	7765.105	3020.95	12189.42	6387.9954	643.3341844	502.8414098	936.526	4196.143936	7476.114128
5586	5397.74	7776.685	3018.42	12233.84	6416.885556	645.5939862	508.4413335	927.842	4207.905435	7481.79499
5523	5436.05	7772.947	3002.42	12242	6416.726935	639.889101	516.7228713	900.421	4194.793138	7471.348208
5364	5389.32	7731.895	3012.16	12145.58	6418.182967	641.6220872	515.0222724	870	4182.263023	7466.597077
5426	5273.84	7596.895	2964.95	11914.95	6382.990399	646.6139897	509.7884065	816.105	4194.15042	7435.112583
5536	5394.32	7717.421	3001.58	12131.79	6362.630747	629.7886196	503.2359708	801.632	4154.344896	7370.965796
5413	5381.42	7744.895	3006.21	12128.79	6338.235148	632.9900659	501.3141998	780.474	4152.460108	7363.109365
5458	5410.32	7780.316	3029.79	12206.63	6358.229893	634.1187395	501.0136654	769.368	4182.782313	7393.383459
5465	5306.16	7653.632	2974.42	12018.16	6281.205425	623.5288094	493.0420083	729.579	4153.44594	7317.951865
5334	5358.42	7689.053	2998.26	12093.16	6245.640476	622.5809258	494.8137343	672.316	4230.345792	7313.07739
5355	5358.58	7661	2963.58	12019.53	6286.925813	621.2932218	504.4494736	624.263	4228.385881	7301.190193

5409	5390.16	7773.21	3039.95	12149	6246.612688	624.5155829	505.048511	572.421	4225.481997	7273.754377
5370	5260.68	7593.79	2958.74	11941.95	6208.197431	623.2473395	494.6888196	507.579	4210.056511	7220.872725
5308	5347.42	7706.316	3009.16	12041.89	6196.341083	627.3701768	483.0886133	463.263	4214.733249	7162.420852
5355	5326.05	7680.158	2966	11999.05	6196.322691	610.2620754	491.6213912	419.526	4211.062836	7186.996285
5406	5330.95	7674.842	2998.32	12039	6262.757011	618.9503812	488.0107459	373.842	4288.213268	7246.826566
5212	5232.21	7565.21	2931.95	11867.79	6253.464989	623.2716188	488.7672541	354.368	4321.521747	7249.207032
5220	5301.79	7623.684	2966.37	11897.16	6192.436575	622.3748311	476.3218043	358.316	4222.591724	7156.16806
5232	5272.68	7653.895	2963.74	11916.16	6164.643377	604.7490039	496.6713881	361.842	4275.020406	7147.160701
5280	5299.58	7652.158	2969.84	11942.16	6182.349221	609.3661326	488.9883149	366.632	4276.766275	7122.03417
5221	5280.63	7627.474	2968.74	11902.26	6203.99286	612.8202036	483.6235201	379	4219.168612	7093.966603
5151	5253.47	7607.684	2952.16	11852.42	6126.688043	612.5622511	468.9604074	376.421	4218.630188	7054.854482
5223	5243.26	7560.737	2965.11	11799.58	6106.319593	608.3437632	468.2669653	375.684	4185.563598	7018.937569
5145	5206.89	7527.421	2903.21	11750.79	6123.22573	614.8404767	473.5974562	370.053	4148.878394	7007.338109
5151	5230.79	7560.105	2929.58	11810.42	6128	616.778	474.889	359.053	4141.25	7005.999512

Appendix II (electronic version only)

Raw data of elemental mapping of dinosaur eggshells.

Thickness (µm)	*Triprismatoolithus* Ca	*Triprismatoolithus* P	Thickness (µm)	*Macroolithus* Jiangxi Ca	*Macroolithus* Jiangxi P	Thickness (µm)	*Macroolithus* Henan Ca	*Macroolithus* Henan P	Thickness (µm)	*Macroolithus* Guangdong Ca	*Macroolithus* Guangdong P
1	450	2	1	4931	6	0	12775	5	0	4576	2
2	488	7	2	11863	10	1.01	12692	6	1.02	10925	2
3	754	10	3	15206	6	2.02	12705	8	2.03	10427	1
4	684	13	4	16954	3	3.03	12987	3	3.05	12079	5
5	693	8	5	18932	10	4.04	12477	8	4.06	12922	5
6	1010	14	6	19758	15	5.05	12717	3	5.08	12520	5
7	1770	34	7	21157	23	6.06	12940	9	6.1	11543	1
8	5558	17	8	21665	13	7.07	13123	15	7.11	12991	2
9	8266	24	9	21631	18	8.09	13466	9	8.13	13039	6
10	16897	41	10	21257	15	9.1	13178	16	9.14	13326	3
11	18153	39	11	21678	15	10.11	12652	12	10.16	13125	6
12	18320	51	12	21387	18	11.12	12026	7	11.18	13017	7
13	23193	43	13	21333	19	12.13	12730	10	12.19	12684	12
14	23007	34	14	21920	16	13.14	12862	8	13.21	12945	3
15	22623	31	15	22086	16	14.15	13075	8	14.22	13403	9
16	22867	52	16	21915	17	15.16	13296	7	15.24	12989	8
17	22207	35	17	21749	19	16.17	13267	9	16.25	12833	9
18	22398	51	18	21414	20	17.18	13188	6	17.27	12844	17
19	22544	34	19	22257	25	18.19	13158	6	18.29	12528	9
20	22405	41	20	23068	13	19.2	13174	7	19.3	9869	11
21	20342	39	21	22601	23	20.21	13688	10	20.32	9277	7
22	23109	46	22	22720	16	21.22	13425	4	21.33	11921	6
23	23022	45	23	22547	21	22.23	13284	9	22.35	12838	8
24	23041	44	24	22389	14	23.24	12836	14	23.37	13122	4
25	23208	47	25	21563	12	24.26	12797	1	24.38	13117	9
26	23195	44	26	22148	17	25.27	12798	16	25.4	13347	7
27	23112	31	27	22613	21	26.28	12935	13	26.41	13299	9

28	22972	42	28	22242	23	27.29	13041	16	27.43	13032	4
29	23499	34	29	22616	18	28.3	12750	10	28.45	13061	7
30	23546	43	30	22860	15	29.31	12920	11	29.46	12810	7
31	22932	43	31	22155	20	30.32	13103	9	30.48	12860	9
32	23270	48	32	21772	15	31.33	13129	13	31.49	13148	9
33	23746	39	33	21863	25	32.34	13121	6	32.51	13179	15
34	23332	38	34	22375	36	33.35	13160	9	33.53	13381	5
35	23736	34	35	22279	23	34.36	13135	3	34.54	13426	10
36	23141	37	36	22484	24	35.37	13109	9	35.56	13010	8
37	22202	41	37	22255	31	36.38	13141	9	36.57	13007	6
38	23310	47	38	22161	30	37.39	13099	10	37.59	13148	9
39	22693	42	39	22636	29	38.4	12892	16	38.61	12990	13
40	22816	37	40	21857	16	39.41	13210	8	39.62	13358	5
41	22696	46	41	22550	33	40.43	13005	13	40.64	13237	14
42	22182	42	42	22784	16	41.44	12836	8	41.65	13194	9
43	22461	34	43	22129	22	42.45	12830	9	42.67	13572	8
44	21976	35	44	22368	27	43.46	13216	11	43.68	13320	5
45	22136	41	45	21523	27	44.47	13230	8	44.7	13510	3
46	21947	32	46	21571	27	45.48	13039	6	45.72	13051	10
47	22274	35	47	21708	29	46.49	13152	9	46.73	12533	7
48	22450	45	48	22755	25	47.5	13226	14	47.75	12624	9
49	22807	36	49	22459	31	48.51	13220	5	48.76	13064	8
50	23115	38	50	22772	39	49.52	13252	9	49.78	13040	12
51	23142	28	51	23081	38	50.53	13056	10	50.8	13083	23
52	22854	33	52	22729	39	51.54	12881	11	51.81	13184	8
53	22239	44	53	22815	36	52.55	12487	13	52.83	13137	18
54	21495	36	54	22504	40	53.56	12785	5	53.84	13256	9
55	21959	41	55	22160	20	54.57	13208	5	54.86	13143	7
56	22349	30	56	22524	25	55.58	13594	7	55.88	12584	10
57	22691	36	57	22505	24	56.6	13477	6	56.89	12092	5
58	22582	30	58	22555	43	57.61	13268	10	57.91	13166	7
59	23193	51	59	22834	34	58.62	12891	11	58.92	13286	10
60	23581	41	60	22806	27	59.63	12993	10	59.94	13071	12
61	22976	26	61	22850	20	60.64	12989	13	60.96	13010	10
62	22716	29	62	22457	30	61.65	13285	13	61.97	13137	8
63	23572	40	63	22329	37	62.66	13589	4	62.99	13265	8
64	24090	37	64	22342	29	63.67	13548	11	64	13166	9

65	23466	40	65	22317	29	64.68	13731	16	65.02	13217	13
66	23487	44	66	22276	25	65.69	13469	9	66.04	12847	8
67	23096	30	67	23007	33	66.7	13186	14	67.05	13045	31
68	23608	44	68	23302	26	67.71	12934	13	68.07	12750	46
69	23978	48	69	22589	34	68.72	12959	5	69.08	12776	24
70	24021	27	70	22989	37	69.73	12512	8	70.1	13171	20
71	23926	43	71	23021	29	70.74	12526	14	71.11	13147	13
72	23754	26	72	22704	37	71.75	12894	14	72.13	13078	10
73	23209	39	73	22298	32	72.77	13582	10	73.15	12768	12
74	24188	43	74	22320	31	73.78	13216	13	74.16	12889	9
75	24353	33	75	22640	38	74.79	12623	14	75.18	12860	7
76	24050	40	76	23105	33	75.8	12597	11	76.19	13020	9
77	23861	47	77	23163	43	76.81	12884	8	77.21	13008	6
78	23521	49	78	23378	28	77.82	12987	13	78.23	13035	14
79	23418	53	79	23096	28	78.83	12856	8	79.24	12977	20
80	23479	59	80	23002	30	79.84	12726	10	80.26	13120	11
81	22953	68	81	22801	44	80.85	13015	7	81.27	13116	19
82	23964	39	82	21383	38	81.86	13038	7	82.29	13115	12
83	23628	48	83	21777	33	82.87	13196	4	83.31	13422	8
84	23020	35	84	22337	46	83.88	13050	7	84.32	13510	9
85	22316	29	85	22149	52	84.89	13379	3	85.34	13462	14
86	23093	38	86	22393	44	85.9	12785	7	86.35	13158	13
87	23345	30	87	21949	39	86.91	12496	11	87.37	12692	14
88	23585	41	88	22834	33	87.93	12529	8	88.39	12823	8
89	23358	35	89	23406	27	88.94	12390	15	89.4	12137	9
90	23541	32	90	23249	38	89.95	12691	14	90.42	11872	8
91	23313	28	91	22730	50	90.96	12887	3	91.43	11864	12
92	23230	30	92	23005	45	91.97	13122	8	92.45	12214	17
93	23502	23	93	23250	46	92.98	13164	20	93.47	12642	8
94	23013	29	94	22572	51	93.99	13109	11	94.48	12985	11
95	23401	32	95	22082	41	95	12915	13	95.5	12866	18
96	23382	21	96	22631	44	96.01	12746	13	96.51	12912	13
97	23762	36	97	22717	41	97.02	12814	13	97.53	12808	9
98	24353	34	98	22247	36	98.03	12923	2	98.54	13147	4
99	24348	33	99	22688	32	99.04	13161	14	99.56	13033	3
100	24024	29	100	22556	47	100.05	13188	7	100.58	13394	3
101	23591	24	101	21135	45	101.06	13279	11	101.59	13181	3

102	23036	23	102	22333	35	102.07	13125	14	102.61	13203	7
103	22848	16	103	22321	45	103.08	13021	12	103.62	12887	8
104	21856	13	104	21718	38	104.1	13636	11	104.64	13009	4
105	22514	16	105	20115	40	105.11	13549	12	105.66	12963	7
106	22968	9	106	21648	36	106.12	13185	13	106.67	12870	6
107	22119	14	107	22328	33	107.13	13081	6	107.69	13049	5
108	13344	14	108	22584	52	108.14	13198	11	108.7	12777	9
109	19342	12	109	22651	43	109.15	13285	6	109.72	12774	10
110	22622	8	110	21811	51	110.16	13114	10	110.74	13385	16
111	21615	27	111	22053	50	111.17	13074	9	111.75	13226	5
112	21216	13	112	22673	55	112.18	13043	8	112.77	13501	6
113	21633	6	113	19193	34	113.19	13398	9	113.78	13435	8
114	22622	8	114	17600	42	114.2	12765	7	114.8	13750	6
115	23690	16	115	21775	52	115.21	12984	7	115.82	13451	3
116	23610	20	116	21802	21	116.22	12846	5	116.83	13197	14
117	22504	15	117	21510	31	117.23	12277	14	117.85	13138	9
118	21810	26	118	22857	48	118.24	12988	9	118.86	13296	7
119	22502	17	119	22601	49	119.25	12915	10	119.88	13138	6
120	22346	22	120	23029	56	120.27	12645	14	120.9	13129	13
121	22271	17	121	23349	50	121.28	13112	14	121.91	13142	7
122	22502	16	122	23330	51	122.29	13042	18	122.93	13250	7
123	22241	15	123	22665	61	123.3	13225	13	123.94	13355	7
124	23347	15	124	23263	56	124.31	13060	14	124.96	13149	4
125	23607	17	125	23126	66	125.32	13282	12	125.97	12938	6
126	22919	23	126	23745	44	126.33	12771	9	126.99	13334	6
127	23364	23	127	22803	50	127.34	12832	17	128.01	13274	5
128	22163	22	128	22257	38	128.35	12866	14	129.02	13393	8
129	22857	15	129	23000	47	129.36	12927	13	130.04	13252	7
130	22815	27	130	22706	45	130.37	13208	16	131.05	13363	6
131	22893	19	131	23167	56	131.38	13437	11	132.07	13405	4
132	23325	23	132	22815	42	132.39	13372	11	133.09	13212	5
133	23547	35	133	22627	44	133.4	13237	13	134.1	13085	11
134	23129	37	134	22780	36	134.41	13306	10	135.12	13208	8
135	23063	36	135	22555	32	135.42	13388	11	136.13	12964	3
136	21185	26	136	23235	49	136.44	13085	5	137.15	12670	9
137	21836	35	137	23184	40	137.45	13374	17	138.17	12762	7
138	22414	32	138	23077	50	138.46	13156	10	139.18	13230	3

139	22631	36	139	23115	34	139.47	12816	13	140.2	12880	5
140	23449	33	140	22460	31	140.48	12953	11	141.21	13149	9
141	23864	18	141	23019	39	141.49	12910	14	142.23	13073	8
142	22876	28	142	22720	36	142.5	13106	14	143.25	13251	6
143	23195	30	143	22555	26	143.51	12871	14	144.26	13098	11
144	23334	27	144	23416	30	144.52	13124	14	145.28	13118	15
145	23268	14	145	21984	25	145.53	13256	9	146.29	13024	4
146	21225	36	146	22729	18	146.54	13331	11	147.31	12983	6
147	20304	12	147	22920	22	147.55	13261	14	148.33	13018	4
148	21583	27	148	22803	46	148.56	13248	12	149.34	13167	7
149	21623	26	149	22669	49	149.57	13268	17	150.36	13327	6
150	21646	20	150	22464	42	150.58	13014	21	151.37	13230	7
151	22542	22	151	22930	54	151.59	12096	12	152.39	13423	4
152	22228	27	152	24169	49	152.61	11795	7	153.4	13478	6
153	21428	29	153	22809	56	153.62	12984	13	154.42	13336	5
154	22494	24	154	22555	43	154.63	12958	23	155.44	13256	10
155	22190	35	155	22393	40	155.64	13602	16	156.45	13067	12
156	20142	43	156	23008	45	156.65	13486	12	157.47	12933	15
157	21601	45	157	22368	40	157.66	13452	17	158.48	12906	10
158	20780	33	158	22529	38	158.67	13089	10	159.5	13306	13
159	20143	30	159	22583	48	159.68	13363	20	160.52	13329	5
160	20744	41	160	22296	35	160.69	13200	9	161.53	13405	5
161	20375	44	161	21718	26	161.7	13370	23	162.55	13285	8
162	19984	47	162	21159	10	162.71	13250	10	163.56	13402	8
163	19736	48	163	21070	26	163.72	13022	10	164.58	13656	7
164	20936	39	164	21587	24	164.73	13154	8	165.6	13325	4
165	22750	52	165	21907	27	165.74	13570	12	166.61	13279	8
166	22749	62	166	21326	13	166.75	13322	12	167.63	13166	5
167	22492	45	167	21821	3	167.77	12990	12	168.64	13439	9
168	22784	42	168	20085	8	168.78	12808	12	169.66	13460	3
169	21685	33	169	17430	6	169.79	13128	11	170.68	13169	6
170	15585	28	170	19223	20	170.8	13432	20	171.69	13087	7
171	17402	18	171	21481	31	171.81	13449	16	172.71	12835	6
172	22888	38	172	19183	44	172.82	13150	8	173.72	12823	1
173	21028	36	173	14086	35	173.83	13006	8	174.74	13044	4
174	19975	21	174	10825	15	174.84	13015	10	175.76	13000	3
175	19862	12	175	17225	12	175.85	12904	15	176.77	13135	2

176	20304	26	176	22833	42	176.86	12774	18	177.79	13295	2
177	20987	36	177	23548	53	177.87	12744	16	178.8	13459	7
178	17846	31	178	23968	43	178.88	12606	8	179.82	13375	2
179	21390	37	179	23668	40	179.89	12835	8	180.83	12907	6
180	20491	33	180	23400	31	180.9	12857	9	181.85	13074	9
181	22366	26	181	22194	45	181.91	12614	16	182.87	12450	8
182	22210	26	182	23089	40	182.92	13120	17	183.88	12356	7
183	20085	27	183	22011	39	183.94	13331	16	184.9	12623	10
184	15439	27	184	21881	23	184.95	13429	9	185.91	12676	11
185	15163	29	185	22391	51	185.96	13575	16	186.93	12942	16
186	17098	27	186	23084	51	186.97	13654	12	187.95	13134	5
187	21807	31	187	23164	53	187.98	13270	11	188.96	12659	10
188	22762	26	188	22904	49	188.99	13402	17	189.98	13223	18
189	22457	22	189	21983	51	190	13507	20	190.99	13090	8
190	22588	31	190	19728	39	191.01	13653	14	192.01	13317	5
191	22520	32	191	20463	31	192.02	13946	6	193.03	13176	5
192	22641	39	192	22467	26	193.03	13281	19	194.04	12951	9
193	23036	33	193	22925	44	194.04	13113	13	195.06	12887	2
194	22869	32	194	22346	37	195.05	13368	20	196.07	12847	6
195	23100	30	195	22557	44	196.06	13445	16	197.09	13072	3
196	23108	30	196	23118	39	197.07	13240	11	198.11	13006	8
197	22992	32	197	22406	39	198.08	13048	10	199.12	13426	1
198	22990	42	198	22188	46	199.09	13502	6	200.14	13600	3
199	23106	35	199	22508	31	200.11	13287	16	201.15	13563	5
200	23423	49	200	22537	35	201.12	13252	16	202.17	13536	9
201	23539	45	201	22792	39	202.13	13007	12	203.19	13608	10
202	23772	40	202	22595	38	203.14	13043	5	204.2	13404	10
203	23359	37	203	17199	31	204.15	13084	10	205.22	13287	2
204	23159	33	204	5275	9	205.16	13722	14	206.23	13295	4
205	23130	41	205	10187	12	206.17	13336	6	207.25	13420	4
206	23024	37	206	20168	14	207.18	13422	10	208.26	13395	11
207	23474	34	207	21985	30	208.19	13369	11	209.28	12817	9
208	23237	42	208	23264	40	209.2	12913	10	210.3	12912	6
209	23350	45	209	22998	37	210.21	12820	14	211.31	13099	6
210	23281	40	210	22567	38	211.22	12825	10	212.33	13234	11
211	23601	34	211	22503	38	212.23	13199	13	213.34	12924	7
212	23976	47	212	22349	38	213.24	13165	12	214.36	13256	9

213	23814	53	213	22903	31	214.25	13171	12	215.38	13195	5
214	23620	46	214	22856	33	215.26	13424	23	216.39	13391	7
215	22683	40	215	22726	37	216.28	13633	13	217.41	13259	6
216	23192	47	216	22723	40	217.29	13317	16	218.42	13291	9
217	22904	33	217	22908	41	218.3	13212	4	219.44	13495	8
218	22997	36	218	22048	46	219.31	13229	13	220.46	13089	6
219	22549	39	219	21694	38	220.32	13788	5	221.47	12952	7
220	22768	32	220	22211	52	221.33	13871	13	222.49	13238	7
221	23023	31	221	22351	39	222.34	13519	9	223.5	13229	9
222	23097	25	222	22606	39	223.35	13191	12	224.52	13372	6
223	23492	33	223	22018	42	224.36	13181	13	225.54	13101	15
224	23360	37	224	22069	34	225.37	13272	15	226.55	12872	15
225	23799	28	225	22406	33	226.38	13337	9	227.57	13282	11
226	21596	38	226	22466	35	227.39	13262	5	228.58	13273	6
227	20920	31	227	23414	42	228.4	12855	10	229.6	13150	6
228	21315	30	228	22936	43	229.41	12943	10	230.62	13110	8
229	22730	25	229	22803	49	230.42	13089	12	231.63	12832	7
230	23377	28	230	23110	40	231.43	13538	13	232.65	12832	9
231	22935	36	231	22765	41	232.45	13302	5	233.66	12950	10
232	23320	36	232	22406	49	233.46	13199	6	234.68	13149	11
233	22580	25	233	23345	41	234.47	13191	15	235.69	13438	11
234	17904	24	234	22928	49	235.48	13393	12	236.71	13091	8
235	21886	19	235	23203	43	236.49	13127	16	237.73	13245	9
236	22584	26	236	22588	40	237.5	13260	17	238.74	13425	12
237	22128	32	237	22286	55	238.51	13509	6	239.76	13313	5
238	23183	27	238	22469	43	239.52	13369	7	240.77	12645	10
239	22954	25	239	22487	53	240.53	13396	8	241.79	12915	11
240	22925	31	240	22804	53	241.54	13553	9	242.81	12931	7
241	23240	19	241	23167	44	242.55	13413	7	243.82	13133	11
242	23495	47	242	22951	45	243.56	13282	6	244.84	13334	6
243	23573	43	243	22936	44	244.57	13433	8	245.85	13270	9
244	23681	31	244	23287	53	245.58	12899	16	246.87	13307	14
245	23490	36	245	23187	37	246.59	13252	16	247.89	13073	9
246	23655	45	246	21236	52	247.61	13271	11	248.9	13216	10
247	23956	27	247	6361	19	248.62	13255	10	249.92	13237	5
248	24004	40	248	15449	19	249.63	13388	11	250.93	13052	12
249	23525	37	249	22562	48	250.64	13487	8	251.95	13117	5

250	23598	42	250	23090	39	251.65	13545	7	252.97	12954	8
251	23758	26	251	22142	50	252.66	13408	10	253.98	13036	7
252	23616	44	252	23487	51	253.67	13009	10	255	13294	12
253	23484	37	253	23105	55	254.68	13161	4	256.01	13420	9
254	23793	42	254	22047	46	255.69	13165	18	257.03	13470	5
255	23765	32	255	22201	41	256.7	13257	17	258.05	13424	5
256	23302	34	256	22882	36	257.71	13266	5	259.06	13398	4
257	23035	30	257	23155	68	258.72	13207	16	260.08	13340	2
258	22904	27	258	23527	49	259.73	13484	5	261.09	13146	2
259	22782	33	259	22799	35	260.74	13283	12	262.11	13494	9
260	23042	35	260	22263	36	261.75	12177	20	263.12	13473	7
261	23630	30	261	22924	43	262.76	11654	8	264.14	13152	4
262	23597	39	262	23873	46	263.78	11541	16	265.16	13196	2
263	23362	28	263	22623	31	264.79	12846	12	266.17	13293	7
264	22962	29	264	22318	48	265.8	13267	11	267.19	13373	5
265	22526	37	265	22204	51	266.81	13415	11	268.2	13272	10
266	22929	48	266	22645	52	267.82	13241	17	269.22	13357	5
267	23040	27	267	22624	56	268.83	13266	10	270.24	13225	6
268	23137	41	268	22450	49	269.84	13058	5	271.25	13376	14
269	23525	36	269	22427	66	270.85	12951	11	272.27	13297	12
270	23347	28	270	22564	43	271.86	13242	11	273.28	13072	5
271	23016	37	271	22410	46	272.87	13395	12	274.3	13165	8
272	22753	32	272	22632	47	273.88	13338	9	275.32	13132	5
273	23213	37	273	22747	47	274.89	13300	10	276.33	13393	8
274	23273	38	274	22674	41	275.9	13370	19	277.35	13181	6
275	22606	35	275	22859	45	276.91	13116	10	278.36	13231	6
276	21009	34	276	23293	42	277.92	13093	15	279.38	12792	3
277	10515	18	277	22639	33	278.93	12459	7	280.4	13054	6
278	17252	30	278	23235	40	279.95	13062	8	281.41	12936	6
279	21478	42	279	23661	50	280.96	13006	10	282.43	13274	8
280	21970	31	280	23437	39	281.97	13255	10	283.44	13174	4
281	22447	39	281	24014	32	282.98	13125	20	284.46	13357	5
282	22732	34	282	22706	51	283.99	13332	14	285.48	12815	7
283	22725	33	283	22443	62	285	13384	9	286.49	13128	11
284	22026	45	284	22702	29	286.01	13478	10	287.51	13240	6
285	23090	45	285	22960	44	287.02	13246	9	288.52	13164	6
286	23603	45	286	22130	31	288.03	13171	5	289.54	13375	7

287	23206	39	287	22568	44	289.04	13211	13	290.55	13200	7
288	23600	38	288	20259	42	290.05	13292	13	291.57	13549	8
289	23885	47	289	22530	44	291.06	13293	15	292.59	13203	6
290	23475	41	290	22731	41	292.07	13435	16	293.6	12985	14
291	23183	45	291	22229	39	293.08	12992	14	294.62	13247	13
292	23181	28	292	22364	43	294.09	13379	19	295.63	13154	9
293	23333	35	293	22950	45	295.1	13095	18	296.65	12932	7
294	23113	30	294	23663	34	296.12	12827	15	297.67	12803	9
295	23585	44	295	23668	30	297.13	13054	11	298.68	12739	7
296	23270	40	296	22304	33	298.14	13479	8	299.7	13095	7
297	23393	42	297	22932	43	299.15	13586	10	300.71	13373	7
298	22848	43	298	22786	31	300.16	13353	14	301.73	13541	6
299	21643	41	299	22782	32	301.17	13372	16	302.75	13651	8
300	23052	43	300	22835	35	302.18	13511	9	303.76	13757	14
301	23105	40	301	22962	34	303.19	13063	17	304.78	13714	6
302	22998	34	302	23076	47	304.2	13007	14	305.79	13379	3
303	23440	35	303	22716	33	305.21	13498	11	306.81	13403	11
304	22912	39	304	22373	38	306.22	13336	16	307.83	13371	8
305	23557	37	305	23001	48	307.23	13744	4	308.84	13318	7
306	23461	37	306	22707	44	308.24	13721	2	309.86	13675	7
307	23122	34	307	22778	48	309.25	13421	8	310.87	13391	5
308	22867	44	308	22598	38	310.26	13674	14	311.89	13731	9
309	23091	34	309	22368	23	311.27	13676	16	312.91	13220	12
310	23760	35	310	22681	33	312.29	13668	11	313.92	13224	11
311	23886	44	311	23407	31	313.3	13901	10	314.94	13225	7
312	23776	44	312	23589	37	314.31	13878	11	315.95	12756	9
313	23773	39	313	23491	25	315.32	13240	13	316.97	13101	9
314	23750	38	314	22942	18	316.33	12041	14	317.98	13005	20
315	24277	21	315	22837	19	317.34	9564	13	319	12812	14
316	23655	24	316	22597	33	318.35	11076	3	320.02	13030	16
317	23308	39	317	21975	23	319.36	12979	10	321.03	13325	9
318	23666	34	318	21132	17	320.37	13277	4	322.05	13258	8
319	23928	45	319	22016	9	321.38	13400	7	323.06	13318	7
320	23570	34	320	22205	12	322.39	13846	16	324.08	13566	4
321	22545	39	321	23403	5	323.4	13691	16	325.1	13167	10
322	22680	23	322	22297	30	324.41	13169	10	326.11	12946	8
323	22617	38	323	22869	36	325.42	12719	12	327.13	12872	6

324	22257	29	324	23012	44	326.43	12935	7	328.14	12782	7
325	22580	27	325	22793	39	327.45	13219	12	329.16	12745	9
326	22920	34	326	22309	47	328.46	12971	9	330.18	12914	10
327	22965	55	327	22423	34	329.47	13161	17	331.19	12892	6
328	22558	29	328	23160	37	330.48	13192	12	332.21	13103	6
329	23817	32	329	23172	26	331.49	13338	12	333.22	13291	11
330	23513	34	330	22595	27	332.5	13308	14	334.24	13194	4
331	23407	24	331	22872	61	333.51	13321	20	335.26	13496	5
332	23244	28	332	22980	41	334.52	13153	21	336.27	13525	2
333	22993	38	333	22925	56	335.53	13235	18	337.29	13289	7
334	22646	34	334	23542	67	336.54	13423	10	338.3	13138	3
335	22665	50	335	23615	46	337.55	13525	17	339.32	13207	0
336	22261	32	336	21628	56	338.56	13314	9	340.34	13050	11
337	22778	35	337	22488	47	339.57	13334	9	341.35	13102	8
338	18117	43	338	22834	36	340.58	13433	14	342.37	13407	7
339	22479	31	339	22969	36	341.59	13406	9	343.38	13273	4
340	22842	47	340	22238	29	342.6	13530	15	344.4	12981	7
341	22581	37	341	22729	47	343.62	13537	15	345.41	13191	3
342	23121	32	342	22530	30	344.63	13268	19	346.43	13329	5
343	22883	35	343	22398	31	345.64	12979	15	347.45	13493	4
344	22881	27	344	22353	41	346.65	13043	12	348.46	13548	5
345	23145	41	345	22860	42	347.66	13377	8	349.48	13331	4
346	22949	33	346	23101	35	348.67	13337	7	350.49	13536	5
347	22570	38	347	22665	33	349.68	12575	4	351.51	13238	5
348	22545	36	348	22843	23	350.69	12415	6	352.53	13803	7
349	22702	30	349	22707	25	351.7	13291	16	353.54	13111	14
350	22556	27	350	22485	23	352.71	13306	9	354.56	13125	9
351	22613	33	351	22836	24	353.72	13435	6	355.57	13378	9
352	22923	44	352	22794	37	354.73	13245	5	356.59	13231	11
353	22618	38	353	22004	46	355.74	13064	6	357.61	12952	4
354	22850	42	354	22255	40	356.75	13053	12	358.62	13219	6
355	22622	31	355	22595	40	357.76	13318	18	359.64	12980	8
356	22920	33	356	22284	24	358.77	13463	13	360.65	13415	9
357	23061	41	357	22172	39	359.79	13247	9	361.67	13653	8
358	23609	51	358	22391	46	360.8	13110	17	362.69	13606	7
359	23430	41	359	21872	47	361.81	12998	17	363.7	13515	6
360	23061	26	360	22682	27	362.82	12670	10	364.72	13287	7

361	23344	34	361	22284	21	363.83	13227	9	365.73	13072	10
362	23172	21	362	22418	22	364.84	13126	13	366.75	13097	5
363	23941	35	363	18926	25	365.85	13229	15	367.77	13097	5
364	22573	20	364	12445	21	366.86	13184	8	368.78	13396	2
365	23131	36	365	14356	15	367.87	12875	19	369.8	13644	8
366	22998	37	366	20564	21	368.88	13268	14	370.81	13225	8
367	22499	60	367	22022	29	369.89	13217	12	371.83	13166	9
368	22535	51	368	22478	31	370.9	13537	12	372.84	13187	10
369	22674	38	369	22878	32	371.91	13202	14	373.86	12763	11
370	22521	40	370	22593	31	372.92	13285	19	374.88	12992	12
371	21845	49	371	22137	26	373.93	13146	9	375.89	13143	9
372	22657	66	372	22317	29	374.94	13092	11	376.91	13402	9
373	23076	48	373	22158	25	375.96	12895	15	377.92	13320	10
374	22956	51	374	21444	23	376.97	13140	8	378.94	13302	10
375	23271	54	375	22144	27	377.98	13035	13	379.96	13199	8
376	22763	61	376	22260	25	378.99	12804	14	380.97	12942	5
377	23082	61	377	21668	24	380	12963	20	381.99	12884	10
378	23294	54	378	22439	27	381.01	12595	11	383	13247	10
379	23619	43	379	22663	27	382.02	12722	11	384.02	13294	7
380	24069	30	380	21527	20	383.03	13000	8	385.04	13063	5
381	22812	40	381	22444	29	384.04	12956	20	386.05	13724	7
382	23083	41	382	22358	43	385.05	13065	16	387.07	13494	6
383	23484	34	383	22070	25	386.06	13159	9	388.08	13448	11
384	23910	56	384	23056	37	387.07	13340	17	389.1	13226	11
385	23220	48	385	22655	17	388.08	12919	11	390.12	12995	8
386	23702	54	386	21744	25	389.09	13057	11	391.13	13483	8
387	23108	38	387	22170	29	390.1	13191	13	392.15	13189	9
388	22649	48	388	21203	123	391.11	13318	10	393.16	13304	12
389	22902	48	389	22130	115	392.13	13323	6	394.18	13740	7
390	22714	68	390	21976	22	393.14	12788	7	395.2	13322	2
391	22958	52	391	21349	20	394.15	13063	5	396.21	13383	6
392	23444	32	392	19737	31	395.16	12978	15	397.23	13774	6
393	23141	46	393	12856	19	396.17	12962	11	398.24	13570	6
394	23023	44	394	15312	13	397.18	12777	9	399.26	13304	6
395	22896	47	395	18840	25	398.19	12946	13	400.27	13324	5
396	23408	39	396	20633	30	399.2	13093	7	401.29	13558	8
397	23185	46	397	20674	18	400.21	13263	16	402.31	13629	5

398	22884	42	398	19343	29	401.22	13030	16	403.32	13291	3
399	23476	38	399	17287	11	402.23	12942	14	404.34	12880	3
400	23165	49	400	17116	9	403.24	12673	16	405.35	13466	1
401	23563	61	401	19151	19	404.25	12948	14	406.37	13539	5
402	23272	46	402	18156	24	405.26	13036	17	407.39	13367	4
403	22927	47	403	10280	17	406.27	13056	18	408.4	13411	12
404	22777	58	404	2536	4	407.29	13002	16	409.42	13381	10
405	23100	76	405	6119	6	408.3	12775	11	410.43	13260	9
406	23431	55	406	7312	5	409.31	12552	17	411.45	13170	4
407	23840	56	407	5762	3	410.32	13207	14	412.47	13309	2
408	23818	42	408	6131	20	411.33	13386	18	413.48	13538	6
409	23150	57	409	10247	5	412.34	13170	12	414.5	13320	6
410	22977	68	410	13973	21	413.35	13494	12	415.51	13355	6
411	22916	54	411	15889	22	414.36	13473	18	416.53	13404	10
412	23309	41	412	13021	17	415.37	13624	12	417.55	13220	11
413	23575	52	413	3053	18	416.38	13729	8	418.56	13379	4
414	22900	48	414	931	6	417.39	13505	7	419.58	13272	3
415	23441	57	415	288	4	418.4	13536	5	420.59	13358	5
416	23079	67	416	149	2	419.41	13557	15	421.61	13292	7
417	22411	55	417	124	3	420.42	13628	13	422.63	13127	4
418	22286	55	418	243	5	421.43	13747	11	423.64	13581	7
419	22285	59	419	123	5	422.44	13691	11	424.66	13630	3
420	22950	46	420	653	6	423.46	13717	16	425.67	13556	3
421	22402	51	421	3733	4	424.47	13507	11	426.69	13530	4
422	22691	47	422	2646	6	425.48	13670	7	427.7	13344	14
423	22822	56	423	1006	5	426.49	13719	6	428.72	13406	5
424	22700	44	424	469	4	427.5	13792	11	429.74	13333	8
425	22827	53	425	471	3	428.51	13746	15	430.75	13649	5
426	22684	55	426	1215	2	429.52	13500	13	431.77	13681	4
427	23388	41	427	641	1	430.53	13407	14	432.78	13690	4
428	23532	45	428	651	6	431.54	13738	11	433.8	13377	3
429	23850	54	429	438	5	432.55	13670	9	434.82	13568	6
430	23494	42	430	209	4	433.56	13731	12	435.83	13521	3
431	23243	40	431	227	1	434.57	13423	5	436.85	13184	8
432	23295	43	432	222	3	435.58	13445	9	437.86	13197	3
433	23449	44	433	422	3	436.59	13306	5	438.88	13311	7
434	23876	46	434	112	2	437.6	13459	14	439.9	12984	8

435	23361	46	435	214	3	438.61	13349	4	440.91	13082	4
436	22559	41	436	336	3	439.63	13122	13	441.93	13092	12
437	16637	34	437	206	7	440.64	12918	17	442.94	13093	8
438	21485	36	438	159	6	441.65	13061	5	443.96	13092	3
439	21197	28	439	74	5	442.66	13047	19	444.98	13250	6
440	20414	26	440	62	3	443.67	12567	15	445.99	13587	7
441	21092	45	441	56	3	444.68	12876	12	447.01	13628	6
442	20197	39	442	110	0	445.69	13076	14	448.02	13606	13
443	22278	33	443	163	4	446.7	12954	5	449.04	13431	8
444	22474	43	444	87	3	447.71	12695	23	450.06	13147	8
445	22740	45	445	80	4	448.72	13033	12	451.07	13252	12
446	23290	52	446	118	8	449.73	13135	22	452.09	13649	5
447	23193	34	447	170	1	450.74	13157	23	453.1	13375	2
448	22589	51	448	709	2	451.75	13297	14	454.12	13206	6
449	22286	45	449	282	5	452.76	13132	11	455.13	13255	4
450	21380	45	450	123	7	453.77	13456	20	456.15	13393	5
451	22016	31	451	68	5	454.78	13154	10	457.17	13242	7
452	23164	41	452	35	1	455.8	12978	12	458.18	13487	5
453	22989	41	453	50	3	456.81	13040	8	459.2	13437	9
454	22335	38	454	68	1	457.82	13450	13	460.21	13536	5
455	23377	40	455	72	2	458.83	13118	14	461.23	13233	7
456	22825	37	456	64	1	459.84	12989	11	462.25	13402	4
457	21069	26	457	32	5	460.85	13046	17	463.26	13273	4
458	14822	26	458	39	3	461.86	13185	16	464.28	13090	8
459	12780	22	459	49	3	462.87	12974	12	465.29	13151	5
460	20656	38	460	42	4	463.88	13083	7	466.31	13172	4
461	21366	30	461	57	2	464.89	13045	11	467.33	13317	5
462	21701	40	462	35	4	465.9	13066	13	468.34	13461	7
463	21240	40	463	42	4	466.91	12995	25	469.36	13354	5
464	21790	40	464	35	3	467.92	13248	20	470.37	13166	5
465	22072	29	465	54	2	468.93	13476	14	471.39	13177	6
466	22984	39	466	74	4	469.94	13095	13	472.41	13280	5
467	22515	42	467	60	6	470.95	13528	13	473.42	13415	9
468	23014	42	468	30	3	471.97	13517	6	474.44	13248	7
469	23212	30	469	38	2	472.98	13464	14	475.45	13460	4
470	22799	39	470	38	5	473.99	13055	20	476.47	13323	6
471	19014	39	471	34	3	475	13102	10	477.49	13305	6

472	22347	28	472	52	4	476.01	13213	13	478.5	13551	5
473	22427	47	473	42	1	477.02	12949	9	479.52	13829	4
474	23062	43	474	52	3	478.03	13229	11	480.53	13707	9
475	23347	49	475	55	4	479.04	13450	14	481.55	13578	9
476	22536	41	476	54	3	480.05	13250	10	482.56	13224	5
477	22784	31	477	46	4	481.06	13414	16	483.58	13145	12
478	22609	49	478	41	1	482.07	13106	20	484.6	13274	8
479	23410	48	479	42	5	483.08	13034	16	485.61	13412	2
480	22811	44	480	37	1	484.09	13283	7	486.63	13071	6
481	23485	52	481	55	1	485.1	13156	14	487.64	12887	10
482	23774	47	482	47	4	486.11	13285	17	488.66	13069	5
483	23142	33	483	49	1	487.13	13301	21	489.68	12951	5
484	23454	45	484	45	2	488.14	13236	11	490.69	13287	4
485	23458	53	485	40	7	489.15	13332	15	491.71	13586	7
486	23724	49	486	51	4	490.16	12786	10	492.72	13675	5
487	23460	52	487	67	6	491.17	13226	12	493.74	13499	5
488	23501	54	488	24	4	492.18	13236	10	494.76	13465	12
489	23647	59	489	82	1	493.19	12942	9	495.77	13485	8
490	23497	47	490	54	2	494.2	13046	10	496.79	12984	14
491	22987	36	491	55	4	495.21	13291	13	497.8	13143	7
492	22566	22	492	42	3	496.22	13390	14	498.82	13520	3
493	22336	31				497.23	13281	15	499.84	13528	10
494	22534	32				498.24	13339	8	500.85	13380	7
495	22899	32				499.25	13335	10	501.87	13221	6
496	22969	40				500.26	13301	13	502.88	13283	10
497	23179	39				501.27	13097	10	503.9	12275	13
498	23274	42				502.28	12668	7	504.92	12508	9
499	23350	52				503.3	12918	11	505.93	13353	7
500	23828	49				504.31	13447	10	506.95	12587	16
501	24143	54				505.32	13461	13	507.96	13002	10
502	23502	46				506.33	13444	10	508.98	13150	3
503	23424	45				507.34	13730	13	509.99	13293	7
504	22817	52				508.35	13441	15	511.01	13159	6
505	23033	47				509.36	13544	6	512.03	13323	10
506	23579	58				510.37	13194	11	513.04	13437	11
507	23194	31				511.38	13226	15	514.06	13439	9
508	22842	46				512.39	13235	13	515.07	13637	6

509	23002	42				513.4	13535	8	516.09	13326	7
510	23190	54				514.41	13408	9	517.11	13337	4
511	23093	38				515.42	13279	8	518.12	13087	6
512	22808	36				516.43	13507	12	519.14	11890	12
513	22472	41				517.44	13327	8	520.15	13024	17
514	22808	37				518.45	12966	12	521.17	13442	8
515	23128	36				519.47	12044	8	522.19	13307	7
516	22530	32				520.48	13151	8	523.2	13509	4
517	22606	38				521.49	13091	10	524.22	13516	11
518	23017	49				522.5	13361	15	525.23	13047	8
519	22938	31				523.51	13302	12	526.25	12687	10
520	21984	27				524.52	12840	13	527.27	13058	6
521	22552	50				525.53	12984	11	528.28	13076	4
522	23013	28				526.54	12975	19	529.3	13412	11
523	23035	37				527.55	12680	14	530.31	13453	7
524	23188	17				528.56	12385	19	531.33	13515	7
525	22307	24				529.57	12314	9	532.35	13123	4
526	19397	18				530.58	13237	18	533.36	13299	12
527	17724	16				531.59	13041	10	534.38	13515	12
528	18883	41				532.6	13014	13	535.39	13459	6
529	21050	32				533.61	13000	18	536.41	13426	8
530	21378	38				534.62	13198	9	537.42	13320	4
531	20616	60				535.64	13304	10	538.44	13392	8
532	20253	41				536.65	13018	9	539.46	13427	7
533	20334	31				537.66	13048	9	540.47	13504	8
534	19806	16				538.67	12875	10	541.49	13428	8
535	18879	22				539.68	12866	19	542.5	13129	7
536	18609	48				540.69	13067	16	543.52	13016	8
537	19399	48				541.7	12952	12	544.54	12920	10
538	18851	38				542.71	13095	6	545.55	13157	5
539	18444	38				543.72	13150	14	546.57	13165	7
540	20534	49				544.73	13329	17	547.58	13111	8
541	20667	43				545.74	13403	19	548.6	13007	10
542	20071	49				546.75	13247	19	549.62	12764	3
543	20462	46				547.76	12855	18	550.63	12889	7
544	19082	21				548.77	13190	13	551.65	12836	7
545	19107	24				549.78	13239	12	552.66	13263	10

546	15862	34				550.79	13106	9	553.68	13278	6
547	19516	26				551.81	13006	13	554.7	13552	2
548	22802	19				552.82	13267	14	555.71	13423	2
549	22795	29				553.83	13377	14	556.73	13517	4
550	21827	19				554.84	12933	14	557.74	13304	6
551	23000	16				555.85	13046	13	558.76	13260	7
552	21873	17				556.86	13113	14	559.78	13340	6
553	22803	14				557.87	13250	15	560.79	13510	11
554	21833	14				558.88	13178	9	561.81	13293	12
555	22143	31				559.89	12879	15	562.82	12802	3
556	22446	22				560.9	13247	9	563.84	13043	9
557	23139	48				561.91	13366	12	564.85	13012	5
558	22831	34				562.92	13469	13	565.87	13359	5
559	22902	45				563.93	13263	8	566.89	13295	4
560	23231	46				564.94	13042	10	567.9	13236	6
561	22469	47				565.95	13041	11	568.92	13456	4
562	21740	42				566.97	13288	13	569.93	13401	3
563	22135	44				567.98	13066	15	570.95	13188	3
564	23029	51				568.99	13350	17	571.97	13446	4
565	23047	31				570	13282	17	572.98	13289	5
566	23028	36				571.01	13454	11	574	13252	7
567	22921	30				572.02	13337	12	575.01	13228	4
568	23566	34				573.03	13255	10	576.03	13470	10
569	23487	41				574.04	13126	10	577.05	13296	9
570	23609	52				575.05	13501	13	578.06	13470	7
571	23188	58				576.06	13238	13	579.08	13253	6
572	23004	58				577.07	13305	9	580.09	13546	7
573	23508	54				578.08	13255	9	581.11	13613	4
574	23884	53				579.09	12418	9	582.13	13466	9
575	23734	28				580.1	11512	8	583.14	13480	4
576	23668	45				581.11	13155	18	584.16	13440	6
577	22920	46				582.12	13221	10	585.17	12703	6
578	23526	52				583.14	13211	11	586.19	9456	6
579	22946	66				584.15	13275	15	587.21	8934	6
580	20584	40				585.16	13457	12	588.22	8870	8
581	22958	48				586.17	13335	12	589.24	11926	5
582	23540	45				587.18	12967	14	590.25	13222	10

583	23310	36				588.19	13266	11	591.27	13468	10
584	23343	32				589.2	13100	13	592.28	13299	8
585	24108	33				590.21	12909	14	593.3	13178	3
586	23108	57				591.22	13256	9	594.32	13325	9
587	23535	50				592.23	13298	12	595.33	13197	13
588	23546	37				593.24	12991	13	596.35	13201	4
589	23674	47				594.25	13150	16	597.36	13188	10
590	23815	44				595.26	13120	13	598.38	12915	13
591	24081	55				596.27	12963	18	599.4	13129	10
592	23506	55				597.28	13001	8	600.41	13133	6
593	23644	58				598.29	12953	21	601.43	13334	11
594	23403	38				599.31	12985	10	602.44	13552	8
595	22851	34				600.32	12869	17	603.46	13445	5
596	23002	37				601.33	12996	10	604.48	12767	15
597	22931	47				602.34	12737	20	605.49	12927	12
598	22410	40				603.35	13262	18	606.51	13069	11
599	23680	46				604.36	13258	18	607.52	13226	3
600	23242	30				605.37	13257	12	608.54	13163	11
601	23945	25				606.38	13226	18	609.56	13169	9
602	23727	17				607.39	13288	14	610.57	13340	9
603	23685	19				608.4	13306	10	611.59	13167	6
604	23539	33				609.41	13060	8	612.6	13401	8
605	23448	35				610.42	13005	7	613.62	13506	3
606	23565	45				611.43	13125	10	614.64	13592	2
607	23368	55				612.44	12787	4	615.65	13542	5
608	23368	52				613.45	12902	11	616.67	13139	11
609	23502	41				614.46	12691	9	617.68	13311	6
610	23689	30				615.48	12950	10	618.7	13583	1
611	24280	41				616.49	13465	7	619.71	13500	7
612	23461	40				617.5	13028	9	620.73	12935	4
613	24061	40				618.51	13039	15	621.75	12783	8
614	24240	41				619.52	13088	12	622.76	12831	9
615	23946	29				620.53	13497	12	623.78	12861	8
616	23699	30				621.54	13472	20	624.79	12885	8
617	22706	43				622.55	13264	16	625.81	13450	6
618	22726	54				623.56	13131	13	626.83	13404	5
619	22127	67				624.57	13194	16	627.84	13730	2

620	23329	75				625.58	13179	6	628.86	13708	5
621	23815	53				626.59	13305	15	629.87	13699	3
622	23628	59				627.6	13468	9	630.89	13287	4
623	23589	48				628.61	13329	13	631.91	13269	4
624	23203	41				629.62	13408	6	632.92	13090	7
625	23004	26				630.63	13289	11	633.94	13454	11
626	23408	34				631.65	12869	9	634.95	13608	7
627	23359	30				632.66	13001	9	635.97	13713	3
628	23702	33				633.67	12808	8	636.99	13156	6
629	23189	39				634.68	13341	6	638	13446	5
630	22909	48				635.69	13118	10	639.02	13447	7
631	22508	40				636.7	13125	12	640.03	13348	10
632	22655	61				637.71	12802	15	641.05	13738	4
633	22752	62				638.72	12903	13	642.07	13474	7
634	22645	58				639.73	13003	13	643.08	13466	9
635	22862	52				640.74	13358	7	644.1	13447	5
636	22153	53				641.75	12714	11	645.11	13511	8
637	19490	55				642.76	13262	15	646.13	13641	5
638	22135	40				643.77	13619	6	647.14	13205	7
639	23088	51				644.78	13459	5	648.16	13196	8
640	23302	48				645.79	13099	12	649.18	13297	15
641	22842	58				646.81	13061	9	650.19	13193	7
642	22980	39				647.82	12997	10	651.21	13401	4
643	23592	59				648.83	13124	13	652.22	13505	16
644	23510	44				649.84	12925	11	653.24	13145	6
645	23394	40				650.85	13313	18	654.26	13277	4
646	22926	46				651.86	13404	19	655.27	13118	6
647	22020	39				652.87	13120	11	656.29	13573	5
648	21941	51				653.88	12808	5	657.3	13596	6
649	21708	51				654.89	13080	14	658.32	13224	6
650	22193	58				655.9	12792	7	659.34	13070	8
651	22601	35				656.91	12989	12	660.35	13206	10
652	22805	49				657.92	12753	10	661.37	13331	3
653	23322	43				658.93	13396	11	662.38	13040	4
654	23415	39				659.94	13159	13	663.4	12776	7
655	23380	38				660.95	13071	15	664.42	12883	7
656	23022	34				661.96	12988	16	665.43	13358	7

657	23364	41				662.98	13008	8	666.45	13497	6
658	23030	53				663.99	13052	11	667.46	13444	9
659	23235	58				665	13404	9	668.48	13318	4
660	23634	47				666.01	13289	9	669.5	13428	6
661	23426	64				667.02	13435	9	670.51	13517	9
662	23841	51				668.03	13116	16	671.53	13395	6
663	24020	62				669.04	13468	6	672.54	13174	4
664	24033	36				670.05	13199	9	673.56	13470	9
665	23822	40				671.06	12885	13	674.57	13260	5
666	23465	30				672.07	13243	12	675.59	13416	8
667	22794	53				673.08	12924	18	676.61	13238	14
668	23024	65				674.09	12867	12	677.62	13453	5
669	23809	48				675.1	13129	15	678.64	13775	1
670	23681	59				676.11	13619	8	679.65	13782	11
671	23840	53				677.12	13486	10	680.67	13228	15
672	23702	45				678.13	13581	14	681.69	13236	8
673	23331	70				679.15	12998	10	682.7	13456	8
674	23465	61				680.16	13032	9	683.72	13641	6
675	23934	60				681.17	13231	8	684.73	13599	6
676	23873	58				682.18	13207	8	685.75	13581	1
677	23428	68				683.19	13163	7	686.77	13483	2
678	23604	45				684.2	13421	11	687.78	13523	7
679	23389	50				685.21	13245	8	688.8	12809	6
680	23643	40				686.22	13266	12	689.81	12851	11
681	23565	40				687.23	13372	11	690.83	13429	11
682	24294	39				688.24	13043	13	691.85	13130	13
683	23465	38				689.25	13216	8	692.86	13323	9
684	23482	55				690.26	13064	9	693.88	13444	8
685	23508	49				691.27	13249	12	694.89	13635	6
686	23486	56				692.28	13363	8	695.91	13612	15
687	24054	39				693.29	13499	8	696.93	13658	10
688	24163	38				694.3	13731	7	697.94	13858	4
689	23509	53				695.32	13457	5	698.96	13634	2
690	23132	36				696.33	12986	7	699.97	13661	8
691	19909	53				697.34	12722	11	700.99	13529	7
692	22748	69				698.35	13156	9	702	13481	7
693	23085	52				699.36	13223	9	703.02	13342	6

694	23661	72				700.37	13111	7	704.04	13674	6
695	23714	51				701.38	13326	8	705.05	13461	5
696	24076	48				702.39	13345	11	706.07	13369	4
697	23659	37				703.4	13115	19	707.08	13605	6
698	23185	41				704.41	12987	16	708.1	13840	12
699	23584	32				705.42	13078	7	709.12	13612	4
700	23460	39				706.43	12991	9	710.13	13363	5
701	23748	41				707.44	13195	10	711.15	13735	4
702	23656	61				708.45	13271	12	712.16	13777	6
703	24570	39				709.46	13317	9	713.18	12889	5
704	24404	63				710.48	13182	7	714.2	12421	2
705	24128	50				711.49	13089	9	715.21	13230	12
706	23375	49				712.5	13233	7	716.23	13330	6
707	23562	45				713.51	12945	14	717.24	13384	4
708	22050	39				714.52	12704	8	718.26	13675	8
709	21043	39				715.53	12882	16	719.28	13608	7
710	22892	45				716.54	13049	9	720.29	13332	9
711	23113	54				717.55	12980	13	721.31	13234	4
712	23292	56				718.56	13055	14	722.32	13485	6
713	23200	36				719.57	12949	19	723.34	13304	5
714	23336	49				720.58	13035	16	724.36	13454	8
715	23885	61				721.59	13346	10	725.37	13422	4
716	24167	56				722.6	13393	13	726.39	13312	3
717	23798	58				723.61	13316	13	727.4	13416	12
718	23958	48				724.62	13216	11	728.42	13184	8
719	23193	55				725.63	13244	15	729.43	13041	7
720	22805	71				726.65	13556	9	730.45	13126	10
721	22611	44				727.66	13111	10	731.47	13241	7
722	23477	47				728.67	13127	15	732.48	13247	11
723	23793	37				729.68	13375	15	733.5	13429	4
724	24261	29				730.69	13258	13	734.51	12811	6
725	24467	20				731.7	13188	11	735.53	13173	11
726	23805	24				732.71	13256	9	736.55	13108	10
727	23272	32				733.72	13138	13	737.56	13115	3
728	23267	25				734.73	13264	11	738.58	13073	7
729	23849	19				735.74	13288	13	739.59	12944	5
730	24026	24				736.75	13320	10	740.61	12864	4

731	23796	26				737.76	13527	14	741.63	13033	2
732	23619	29				738.77	13292	10	742.64	13070	4
733	23272	42				739.78	13270	12	743.66	13372	2
734	22787	50				740.79	13186	10	744.67	13046	3
735	23016	36				741.8	13230	11	745.69	13096	5
736	23692	32				742.82	13476	9	746.71	12871	8
737	23610	26				743.83	13678	11	747.72	12889	8
738	22709	34				744.84	13280	10	748.74	12990	9
739	23198	31				745.85	13373	13	749.75	13314	6
740	22582	26				746.86	13493	12	750.77	13427	13
741	23373	32				747.87	13597	16	751.79	13608	4
742	22972	46				748.88	13523	19	752.8	13468	6
743	22709	48				749.89	13530	15	753.82	13191	7
744	21731	37				750.9	13396	14	754.83	13232	4
745	22344	53				751.91	13250	16	755.85	13479	8
746	22769	33				752.92	13449	19	756.86	13375	6
747	22797	51				753.93	13192	15	757.88	13227	4
748	23879	35				754.94	12981	13	758.9	13179	14
749	23871	38				755.95	13245	15	759.91	13018	10
750	23684	31				756.96	13256	12	760.93	13171	4
751	22123	38				757.97	13241	7	761.94	13221	6
752	16229	30				758.99	13361	14	762.96	13524	16
753	7062	20				760	12814	6	763.98	13390	12
754	11825	31				761.01	12863	8	764.99	13392	8
755	13415	34				762.02	13016	5	766.01	13523	9
756	21129	37				763.03	12721	3	767.02	13406	6
757	22883	47				764.04	11714	3	768.04	13293	9
758	23441	35				765.05	10751	1	769.06	13143	9
759	22744	37				766.06	9761	2	770.07	13262	11
760	23112	26				767.07	3633	0	771.09	13224	8
761	23294	43				768.08	509	3	772.1	13376	3
762	23142	42				769.09	375	3	773.12	13217	8
763	22807	44				770.1	646	0	774.14	13172	5
764	23280	41				771.11	672	2	775.15	13433	4
765	22411	30				772.12	376	1	776.17	13242	2
766	18495	34				773.13	338	1	777.18	13166	6
767	23434	27				774.14	423	1	778.2	13179	3

768	23633	24				775.16	206	2	779.22	13157	6
769	23721	32				776.17	260	1	780.23	13340	4
770	23991	26				777.18	161	2	781.25	13248	0
771	23413	29				778.19	175	1	782.26	13296	1
772	23347	22				779.2	182	0	783.28	13673	2
773	23485	32				780.21	238	0	784.29	13589	1
774	23108	43				781.22	264	2	785.31	13324	3
775	23556	24				782.23	242	0	786.33	13603	4
776	23583	17				783.24	352	1	787.34	13074	11
777	23788	44				784.25	425	4	788.36	13163	5
778	23952	32				785.26	778	2	789.37	13528	6
779	23963	46				786.27	2680	4	790.39	13410	7
780	23638	41				787.28	5872	2	791.41	13436	8
781	22957	28				788.29	10271	0	792.42	13536	7
782	22583	41				789.3	11539	2	793.44	13377	5
783	23276	37				790.32	11799	4	794.45	13170	4
784	23547	43				791.33	12324	1	795.47	13118	6
785	23686	42				792.34	12387	6	796.49	13318	7
786	23582	54				793.35	12748	7	797.5	12804	6
787	23556	29				794.36	11492	5	798.52	13195	6
788	23618	38				795.37	6805	1	799.53	13331	6
789	23698	54				796.38	1909	1	800.55	13330	5
790	23721	63				797.39	551	1	801.57	13372	4
791	23697	45				798.4	221	0	802.58	13250	6
792	24246	48				799.41	146	0	803.6	13059	5
793	24072	31				800.42	218	1	804.61	13108	3
794	24114	31				801.43	285	2	805.63	13127	5
795	24343	30				802.44	657	2	806.65	12991	10
796	25016	33				803.45	1985	3	807.66	12914	3
797	24180	22				804.46	8964	3	808.68	12998	11
798	23920	25				805.47	13040	3	809.69	12968	5
799	24010	24				806.49	12863	2	810.71	13251	3
800	23510	13				807.5	13103	4	811.72	12884	6
801	23173	14				808.51	13212	3	812.74	12785	7
802	23425	22				809.52	13228	4	813.76	13420	7
803	23045	26				810.53	13701	4	814.77	13599	5
804	22488	59				811.54	13643	1	815.79	13721	6

805	22588	26				812.55	13616	3	816.8	13596	5
806	22984	66				813.56	12995	0	817.82	13551	5
807	23356	57				814.57	13131	2	818.84	13682	7
808	23692	53				815.58	13164	1	819.85	13493	6
809	23795	43				816.59	13119	3	820.87	13653	2
810	23130	46				817.6	13245	3	821.88	13511	5
811	23262	38				818.61	13170	1	822.9	13425	7
812	22834	39				819.62	13429	2	823.92	13466	10
813	23014	28				820.63	13476	2	824.93	13100	13
814	23338	24				821.64	13194	5	825.95	13469	9
815	22976	22				822.66	12934	0	826.96	13331	3
816	22617	28				823.67	13070	1	827.98	13337	9
817	23073	64				824.68	13134	4	829	13186	9
818	23251	62				825.69	13170	2	830.01	13330	5
819	23275	62				826.7	12894	3	831.03	13591	7
820	22804	51				827.71	13028	1	832.04	13545	3
821	23594	37				828.72	13227	3	833.06	13558	6
822	23836	31				829.73	12183	3	834.08	13289	8
823	23457	23				830.74	10527	4	835.09	13103	4
824	23961	25				831.75	8559	1	836.11	13139	8
825	24279	21				832.76	2361	2	837.12	13077	6
826	23839	15				833.77	1065	0	838.14	12873	6
827	24340	33				834.78	1164	0	839.15	12977	9
828	24415	30							840.17	13043	5
829	23589	30							841.19	13291	3
830	23899	40							842.2	13224	6
831	22817	78							843.22	12725	5
832	23164	65							844.23	13109	9
833	23015	62							845.25	13184	11
834	22601	67							846.27	13129	7
835	22936	62							847.28	13417	1
836	23085	59							848.3	13509	7
837	22487	53							849.31	13185	6
838	20653	41							850.33	13291	11
839	22841	36							851.35	13142	14
840	23242	37							852.36	13308	13
841	23511	48							853.38	13243	10

842	21411	36							854.39	13157	7
843	23166	51							855.41	12915	6
844	22411	62							856.43	13195	7
845	22676	46							857.44	12935	5
846	23141	54							858.46	12953	18
847	23355	57							859.47	13118	4
848	23374	52							860.49	12914	11
849	23893	50							861.51	12748	7
850	23172	47							862.52	12611	9
851	23472	72							863.54	11252	26
852	24071	52							864.55	5245	61
853	23433	27							865.57	945	5
854	23226	53							866.58	328	1
855	23638	61							867.6	437	1
856	23559	58							868.62	310	3
857	22955	44							869.63	241	2
858	23715	59							870.65	337	0
859	22704	56							871.66	336	0
860	22521	55							872.68	167	0
861	23289	32							873.7	125	3
862	23258	51							874.71	134	1
863	23280	53							875.73	194	0
864	22890	51							876.74	159	1
865	23517	65							877.76	172	1
866	23493	44							878.78	155	0
867	22848	46							879.79	113	0
868	22585	56							880.81	117	1
869	22959	45							881.82	165	0
870	22986	55							882.84	135	2
871	22840	38							883.86	137	4
872	22810	40							884.87	234	3
873	22201	50							885.89	1717	1
874	22746	41							886.9	4059	0
875	23733	82							887.92	1194	2
876	24367	45							888.94	482	2
877	24060	51							889.95	242	2
878	24197	43							890.97	224	6

879	24040	45							891.98	725	39
880	23743	48							893	4737	318
881	24049	51							894.01	10355	855
882	23491	48							895.03	11484	1085
883	23905	42							896.05	7402	733
884	24020	36							897.06	2620	246
885	23893	37							898.08	392	36
886	23879	36							899.09	189	5
887	23543	29							900.11	159	0
888	23422	34							901.13	147	2
889	23321	32							902.14	155	2
890	23325	24							903.16	136	2
891	23323	21							904.17	104	3
892	22568	27							905.19	131	0
893	22966	33							906.21	154	2
894	22754	49							907.22	306	1
895	22890	66							908.24	524	4
896	23282	68							909.25	474	2
897	22963	101							910.27	376	3
898	22035	626							911.29	300	1
899	22911	289							912.3	566	1
900	22502	83							913.32	1643	3
901	22817	63							914.33	5016	0
902	23162	48							915.35	10470	1
903	23139	124							916.37	12477	6
904	23263	65							917.38	12287	3
905	23517	63							918.4	12045	4
906	24031	66							919.41	12408	4
907	23547	68							920.43	11617	2
908	23422	77							921.44	12300	5
909	23434	69							922.46	13393	0
910	23795	89							923.48	13289	4
911	23938	89							924.49	13208	3
912	23341	90							925.51	13141	1
913	22542	69							926.52	12211	2
914	22874	44							927.54	7501	3
915	23220	77							928.56	7217	3

916	22853	83							929.57	10986	6
917	22688	67							930.59	12668	1
918	22335	38							931.6	12428	3
919	23686	57							932.62	11007	3
920	21938	25							933.64	11977	5
921	22150	8							934.65	12823	5
922	22271	14							935.67	12379	1
923	22935	7							936.68	11310	2
924	22474	8							937.7	10639	3
925	22392	12							938.72	7918	1
926	22397	12							939.73	5930	0
927	21782	12							940.75	4908	3
928	19639	9									
929	21780	12									
930	22710	15									
931	23419	25									
932	23259	14									
933	23454	9									
934	24134	14									
935	24616	10									
936	24926	11									
937	24041	13									
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939	23121	9									
940	23295	10									
941	23213	6									
942	22749	13									
943	22878	11									
944	23029	5									
945	22736	23									
946	22662	15									
947	22497	12									
948	24174	7									
949	24470	9									
950	23921	9									
951	23932	11									
952	22923	10									

953	23458	8									
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955	24215	14									
956	23748	14									
957	23610	9									
958	22848	4									
959	22414	10									
960	22085	7									
961	21862	7									
962	22067	4									
963	22450	11									
964	23062	13									
965	23717	8									
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967	22918	12									
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969	23735	16									
970	23848	17									
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972	23921	11									
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974	23586	12									
975	24194	5									
976	23895	11									
977	23781	12									
978	23172	16									
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980	24081	20									
981	23254	14									
982	23103	14									
983	22495	11									
984	21768	19									
985	18835	19									
986	20403	29									
987	20040	32									
988	11889	90									
989	5915	169									

990	3979	117									
991	4641	217									
992	8631	501									
993	13114	164									
994	17719	37									
995	19153	21									
996	21381	13									
997	18745	14									
998	11223	26									
999	12273	23									
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1001	4704	35									
1002	1432	27									
1003	1043	23									
1004	1298	29									
1005	1692	27									
1006	3084	38									
1007	3826	26									
1008	3252	27									
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1010	1693	11									
1011	2866	13									
1012	9631	16									
1013	19505	13									
1014	20459	14									
1015	22091	16									
1016	20775	15									
1017	9010	22									
1018	2512	48									
1019	1252	53									
1020	1260	34									
1021	631	35									
1022	597	34									
1023	681	54									
1024	495	19									
1025	369	18									
1026	444	19									

1027	477	10									
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1029	422	38									
1030	368	22									
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1032	9002	14									
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1034	21337	14									
1035	22538	8									
1036	23085	8									
1037	22052	21									
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1044	350	13									
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1047	494	30									
1048	1144	15									
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1051	403	12									
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1053	498	12									
1054	344	28									
1055	321	7									
1056	398	17									
1057	427	13									
1058	339	13									
1059	1122	23									
1060	1315	24									
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1062	399	12									
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1064	414	22									
1065	672	14									
1066	1336	29									
1067	968	13									
1068	292	6									
1069	256	12									
1070	491	10									
1071	569	7									
1072	281	7									
1073	372	6									
1074	476	13									
1075	996	17									
1076	813	14									
1077	631	22									
1078	518	24									
1079	326	10									
1080	374	17									
1081	308	10									
1082	252	5									
1083	323	20									
1084	482	18									
1085	467	12									
1086	477	17									
1087	651	27									
1088	363	16									
1089	335	18									
1090	615	44									
1091	380	21									
1092	376	12									
1093	307	25									
1094	550	96									
1095	656	290									
1096	462	23									
1097	564	14									
1098	536	16									
1099	417	16									
1100	434	23									

1101	504	18									
1102	412	20									
1103	530	30									
1104	540	16									
1105	325	7									
1106	123	11									
1107	204	7									
1108	211	4									
1109	174	7									
1110	181	9									
1111	266	10									
1112	140	9									
1113	394	17									
1114	414	15									
1115	397	12									
1116	549	25									
1117	686	41									
1118	1653	45									
1119	1481	38									
1120	1399	24									
1121	1938	30									
1122	1102	16									
1123	794	12									
1124	441	9									
1125	190	10									
1126	170	6									
1127	299	6									
1128	375	13									
1129	301	10									
1130	408	11									
1131	511	23									
1132	489	22									
1133	419	18									
1134	366	22									
1135	363	13									
1136	619	18									
1137	331	14									

Appendix III (electronic version only)

Oviraptorid dinosaur embryo-containing eggs (SMNH-20140105-1, SMNH-20140105-2, and SMNH-20140105-3)